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SEEDLING RESPONSES OF WHITE SPRUCE PROVENANCES TO SOIL CHEMICAL AND BIOLOGICAL FACTORS

by

BRADLEY NEIL JOHNSON

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

FOREST SOILS

DEPARTMENT OF SOIL SCIENCE

EDMONTON, ALBERTA

SPRING 1986

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled SEEDLING RESPONSES OF WHITE SPRUCE PROVENANCES TO SOIL CHEMICAL AND BIOLOGICAL FACTORS submitted by BRADLEY NEIL JOHNSON in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in FOREST SOILS.

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ABSTRACT

Within a plant species of wide edaphic tolerance, there is often a large amount of genetic variation assorted across the geographic range. The study of ecologically-induced variation (genecology) has been employed for several thousands of years by agriculturalists intent on selecting superior genetic stock for food production. Recently, foresters have recognized the economic benefits possible from programs which isolate superior performers from the wide genetic base of a population.

This study was undertaken to clarify earlier suggestions of soil being an ecological parameter upon which within-species variation in *Picea glauca* (Moench) Voss (white spruce) occurs. As gene pools vary between populations, the physiological basis of variation is of interest. Since the environment is implicated as the cause of this variability, the interplay between adaptive genetic variability and the forces of natural selection, i.e., genotype X environment interactions is studied. The objectives were three-fold: 1. to determine the extent of *Picea glauca* variability in Alberta; 2. to determine whether there are heritable differences between populations due to soil chemical and biological features; 3. where adaptive variations could be separated from random responses, to assess economically useful features of physiological behavior, as in the delineation of seed collection zones.

Seeds representing trees from nine natural stands in three regions of Alberta were grown under glasshouse and growth chamber conditions in three separate tests; one test was designed to elucidate the effects of parental soil chemical and biological properties, while in the other tests, only chemical treatments were applied. Seedling response in each 4- to 7-month test was appraised on the basis of several anatomical and morphological traits.

The results indicated that soil composites of varying pH and dominant cation levels differed in their productivity potential. The calcareous 'Hinton' soil composite was the least receptive rooting environment for all seed sources, with maximal productivity on the most acidic medium from the 'Keg River' region. For all seed sources, seedlings are adapted to the

acidic conditions, provided fungal associations are present. Mycorrhizae, as effective mediators of root physiologic activities, may offer marked protection from aluminum and other heavy metallic cations which may be prominent in the soil solution of the acidic soil type. Apparently, the detrimental effects of the calcareous soil composite cannot be overcome by the presence of mycorrhiza.

As a second trend from the soil composite experiment (experiment 1), biomass production was observed to be greater for Hinton-area provenances, compared to counterparts from the Whitecourt and Keg River areas. Whitecourt families were generally the most inferior. By their ranking of dry weights, Hinton seedlings appear more vigorous in terms of growth potential. These seedlings had consistently high shoot:root ratios and seemed to have a greater emphasis on carbon allocation to the leaves than did the other seed sources. Also, Hinton seed sources, having a lower relative amount of growth inhibition on the Hinton soil treatment, seemingly possessed a broad adaptability to the adversities encountered with soil alkalinity.

With the absence of biologically-mediated nutritional benefits in the hydroponic progeny test, experiment 2, Keg River seed sources exhibited the highest degree of adaptability. When growth in acidic or alkaline nutrient regimes is compared to the neutral case, these provenances displayed smaller decreases than those seedlings from Whitecourt or Hinton.

The results indicated that the performance ranking of Alberta white spruce provenances is dependent on the rooting environment. The presence or absence of biological associations will play a role in performance and, by early indications, Hinton seed sources seem to be superior and more broadly adapted than those from Whitecourt or Keg River if natural soil samples are used. In purely chemical regimes, Keg River provenances exhibited greater adaptability. In terms of root production, Keg River seedlings are most tolerant to Al in sterile hydroponic solutions. Hinton seedlings seemed to be reliant on the presence of soil biotic components, specifically mycorrhizae, to maintain their productivity potential.

The marked variability in productivity potential in Alberta populations reflects a wide genetic base which may be of vital use in tree improvement programs, specifically in the delineation of seed collection zones for reforestation. Any tree improvement program may benefit from the initial search for desirable material including a test of selected families on simulated rooting media. The most positive provenance adaptations could be refined and foresters could benefit by assessing the suitability of various seed sources to a particular soil regime.

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With the completion of this project, there is a debt of gratitude to be paid by the author to numerous individuals. The first to thank are Dr. D.J. Pluth and Dr. B.P. Dancik who, by endless patience and immeasurable academic skill, made the pursuit of this degree an enriching experience. The considered opinions of Dr. G.R. Webster and Dr. R.T. Hardin provided guideance during the evolution of the experiments, and Dr. S. Navratil of the Research Branch, Alberta Forest Service is sincerely appreciated for advice and assistance in developing a mycorrhizae sampling scheme.

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I. INTRODUCTION

Within the plant kingdom, species display differences in their ability to grow and reproduce in various environments. Some are exacting in their requirements for survival while others are far less fastidious, able to grow under a wide range of conditions, having wide edaphic tolerance (Snaydon 1962). Of those whose natural environments are diverse, there is often genetic heterogeneity within the species so that, as Langlet (1979) observed, environmental diversity will be closely paralleled by population diversity. Beginning with mutation and sexual reproduction, evolutionary processess provide genotypic variation and many gene patterns; allelic frequencies at numerous gene loci may respond to natural selection pressures, resulting in the segregation of site-specific adaptively superior gene patterns (Brown *et al* 1972). This within-species heterogeneity ensures that microsite differences will be accomodated over time and space (Meagher 1976).

The interactive behavior of hereditary factors and the physical and chemical environment have been emphasized for as long as agriculturalists have bred and selected plants (Burdon 1977). Through the evaluation of responsive progenies of different plant populations under a variety of field or greenhouse conditions, plant breeders have selected genetic material specifically adapted to one or broadly adapted to more than one field location or condition (Jahroni *et al* 1976). If morphological and physiological differences are retained when the populations are grown in common environments, the populations are termed 'ecotypes'. These ecotypes are not often abruptly separated; rather they are usually members of an 'ecocline', grading into one another on the basis of a continuous variable such as altitude, climate or soil.

Most tree breeding programs, where intra-species variation occurs, employ provenance tests to determine if individuals have broad physiologic homeostasis, or if they are members of distinct physiologic types, each adapted to a narrow range of conditions. The testing of 2 or more genetic entities (provenances) in at least 2 environments allows for the detection of 'genotype x environment' (G X E) interactions, the existence of which implies that the differences in one factor (provenances) differ from levels of the other (environment). The

presence of an interaction, reflected in the differential ranking of genotypes across the environments, assists foresters in weighing the need for using separate seed sources in different environments. If responses of genotypes differ markedly in test conditions, the interactions are considered strong and it may be possible to breed separate, highly adapted populations for specific environments. Faint interactions would suggest any one population may be suited for all outplanting environments (Squillace 1970).

By quantifying the extent to which populations are favored or disfavored in certain environments, seed collection zones may be delineated for the purposes of reforestation. Seed collection zones are described on the basis of parameters measured in provenance tests and are used to minimize the G X E interaction. Concurrent with the G X E decrease, there is a genetic gain increase, a measure of how much better a stand of selected individuals performs relative to a natural stand in the same conditions (Squillace 1970). The eventual outcome of breeding is to produce, within economical limits, tree stands that are uniformly superior to non-selected individuals with respect to phenotypic expression under the test conditions.

The task of differentiating populations on the basis of a select number of traits has a few inherent complications. First, problems arise from the fact that not all traits respond similarily to the same environmental gradient; not all traits follow the same cline (Campbell and Sorenson 1978). Decisions must be made as to the traits used to index the clines. No one individual will meet the superiority standards of all conceivable physical attributes employed in tree improvement. Therefore, any improved population comprising selected genotypes is designated as such only on the basis of the traits used in the selection criteria. With phenotype influenced by the environment and genotype, breeders are interested in economically valuable traits under strong genetic control, i.e. traits with a greater dependence on genetic rather than environmental factors. If such traits of high heritability are monitored, the response to selection can be predicted most accurately (Morgenstern *et al* 1975).

A second problem in the characterization of ecotypes lies in the varied response patterns of provenances to several levels of an environmental factor. Among seed sources, response

curves differ in maxima and minima, hence ranking by their means may vary, depending on the test conditions. The problem is greatest when a ranking is based on the results of test condition, as in a 'common garden' experiment (Campbell and Sorenson 1978). Ideally, more than one test environment should be employed, and each should possess sufficient resolving power to reveal any adaptive genetic variability between populations. If test conditions fail to differentiate the provenances, an inaccurate model of population structure will result.

In this project, the native North American conifer *Picea glauca* (Moench) Voss was evaluated in terms of differentiation across part of its range in Alberta, Canada. The species, commonly referred to as white spruce, is spread over several degrees latitude and longitude, along a wide elevational gradient. Teich and Holst (1974) noted that the tree is present in Canada on soils of varying pH, a fact supported in Alberta by its occurrence on soils ranging in pH from 8.3 to less than 4.5. This observation has led to the formulation of the hypothesis that soil chemical and biological properties exert a selection pressure in the white spruce populations of Alberta and have engrained some degree of genetic uniqueness in the species along its range.

A. Objectives

The overall objective of this project was to measure the responses of progeny, whose parents grew on soils that were diverse with respect to pH levels and associated soil chemical and biological properties. Three separate objectives could be listed as follows:

1. Given the wide range of pH values and the accompanying diversity in chemical composition and microflora, one of the objectives was to determine whether or not biomass accumulation levels would differ on extremely acidic and calcareous soils.
2. Should differences in performance be seen, the intent was to determine if the differences could be interpreted as heritable adaptations to soil chemical and biological parameters.
3. For a third objective, the potential for practical applications are considered. If it could be shown that seedling growth under different chemical regimes was strongly correlated with

seed source, then statements could be made regarding the segregation of this species into edaphic ecotypes. In one possible application of this work, seed sources may be selected for their suitability to the soil. In forests, this may be more practical than amending the soil to fit the capabilites of the plants. Maladaptations of outplanted seedlings may be achieved by testing various provenances for response to different soil biological and chemical media. Any instance of a positive relationship could be exploited for nursery selection, breeding programs and other aspects of reforestation.

Previous researchers (Hanson 1970, Pollard 1973, Rehfeldt 1983) have recommended that seed collection zones be established to reforest lands with progeny whose parents were within specified ranges of elevation and latitude to the outplanting sites. This project will examine the validity of including soil chemical properties as additional criteria in the establishment of such zones. Identification of the specific soil nutrients involved in differentiation may not be possible as factors affecting the solubilization or precipitation of any one ion may also affect other ions. Hence, many nutrients tend to be plentiful or scarce altogether, rather than separately. As well, various ions in the soil solution tend to interact strongly in both field soils and test pots (Goodman 1969). Nonetheless, some studies have forwarded information on the hereditary aspects of plant nutrition. Popp (1984) and Loughman *et al* (1984), working with *Helianthus sp.* and *Armenia meritema* respectively, resolved some genetic differences in the mineral nutrition of these species in sodic, calcareous and acidic habitats. Several adaptive response mechanisms have been theorized to exist.

In an effort to evaluate the potential existence of edaphic ecotypes, three progeny tests were conducted. In one test, seedlings were grown in natural soil composites representing three chemical and biological environments - those of strongly acidic, moderately acidic and alkaline soils. Soil chemical and biological factors were left to impart their influence on growth and productivity. The null hypotheses for this soil composite progeny test were:

1. Soil type does not affect growth performance and survival of white spruce seedlings of differing parental soil type. All families will have consistent phenotypic expression among

all soil treatments. Chemical and biotic regimes will not alter patterns of anatomic development in the seed sources.

2. Analysis of variance will reveal that the patterns of phenotypic expression will be independent of the presence or absence of parental soil conditions. Genotype X environment interactions will not be detected. Consistent superiority of some seed sources on all treatments will show that locally-adapted populations do not exist for the sampled site conditions.

In a second test, seedlings planted on an inert gravel support were differentiated by growth capabilities in response to calcium, magnesium, iron and aluminum levels. With biological influences being minimized, chemical factors alone were implicated as causes of seedling response. From a comparison of the two tests, both biological and chemical influences in the three sampled regions may be determined. The null hypotheses for the gravel culture progeny test were:

1. In the absence of mycorrhizal associations, seed sources will not exhibit discernable differences in the ability to grow in acidic, calcareous and neutral regimes.
2. All seed sources will be similarly affected by the chemistry of the rooting media with no correlations between seed source ranking and the presence or absence of 'parental' conditions.
3. Ranking of families will be patterned after the rankings attained in the soil composite progeny test, indicating an insensitivity of plant metabolic processes to the presence or absence of mycorrhiza.

In a third experiment, seed source response to aluminum only was assessed. Again, solution culture techniques were employed for the benefit of having precise control of the chemical environment presented to the seedling roots. The null hypotheses for the hydroponics progeny test were:

1. The seed sources whose parental habitats are either calcareous or acidic will not incur any deleterious effects by the presence of a moderately low amount of aluminum in a sterile

rooting medium. Compared to an Al-free pot culture, seedling biomass accumulation rates should not be statistically different from the Al treatment.

2. The acidic- and calcareous-originating seed sources will not display significant differences in sensitivity of root metabolic processes to the Al in solution.

Using such tests, one may infer differences in the nutritional requirements among provenances. Statistical analysis of growth measurements and foliage analysis should indicate the potential of each parameter in reflecting the differentiation of white spruce populations in Alberta.

The environments in which the provenances are tested may be compared and evaluated in terms of productivity potential and seed sources may be selected for their superior performance.

II. LITERATURE REVIEW

According to Stern and Roche (1974) climate and soil are the two environmental complexes making up the site of a forest. Soil features, which include the supply of minerals, hydrology, aeration and pH, may be constant or variable over time. Climatic descriptions encompass such parameters as air temperature, precipitation, incipient radiation and photoperiod, linked by latitude, elevation and topographic position. Together, such climatologic and pedologic factors result in a complex web of influences governing plant productivity. After a review of possible responses to these factors, genetic components of plant behavior will be examined, leading to a discussion of how hereditary and environmental factors interrelate.

A. PLANT NUTRITION

A.1. Effect of soil fertility

The effect of soil fertility on plant nutritional status is well documented and multi-faceted. From work in defining optimum nutrient requirements for *Cucurbita* seedlings, Ingestad (1972) interpreted maximum growth rate of a plant as a function of proportions of nutrients, ratios between nitrogen sources and total nutrient content of growth media, with earlier work by Ingestad (1970) revealing what the most desirable ratio for N, P, K, Ca and Mg would be. In addition, his description of growth optima included an account of total nutrient concentration and ratio of ammonium-N and nitrate-N. Ratios of cations are considered to be more crucial in controlling ion uptake than single ion concentrations, because there are ionic interactions in the growth media and competitions for uptake sites on the roots characterized by elemental ratios in tissues (Braakhekke 1984). Examination of nutrients singularly may be deceptive, as a dilution effect in fast growing seedlings yields an apparently lower concentration than in slower growing and possibly less healthy seedlings (Jahroni *et al* 1976).

Further illustrating the effects of nutrient ratios, Johnson *et al* (1980) stated that the total C:total N ratio of the soil may give a good index of N availability, as the amount of carbon contained in litter and root exudates may limit nitrogen mineralization and immobilization rates. Nitrogen availability influences leaf area and root:shoot ratios of *Betula verrucosa* (Ingestad and Lund 1979), therefore growth responses demonstrate the ability of the plant to adapt to nitrogen supply.

Dealing with the effects of nutrient concentrations, Heilman and Ekvan (1980) observed that phosphorous fertilization of *Pseudotsuga menziesii* seedlings increased foliar P levels as much as two-fold while reducing foliar N concentration. They concluded that root:shoot ratios were most affected by amendments affecting soil N levels, a theory supported by Ingestad (1979) who noted an exponential, positive relation between seedling weight and sub-optimal N status and a rapid decrease in the supra-optimal range. In similar work, Armson (1966) saw height growth of white spruce to be under considerable environmental control through the manipulation of N, P, and K fertilizers. Ingestad (1979c) elaborated on the strength of correlation between N level and growth rate, stating that at sub-optimal N levels, K, P, Ca and Mg status may only be of secondary influence; nitrogen was the predominant limiting factor affecting dry matter production.

Several workers have studied the effects of N source on nutrient uptake (McFee and Stone 1968, Ingestad 1979c). In these citations, a preference of spruce and pine for ammonium as the N source was indicated. Increased NH_4^+:NO_3^- ratio increased total N content but resulted in a decreased uptake of other cations, especially potassium. Contradictory evidence of N source preference has been attributed to plant age, pH, cation concentration (Christersson 1972) and also to moisture supply and temperature (Brix and van den Driessche 1974). Van den Driessche and Dangerfield (1975) found that a preference to NH_4^+ is also dependent on the extent of fungal associations, with Douglas-fir seedlings growing on non-sterile solutions preferring ammonium and those in sterile solutions responding best to nitrate. This implies a biological component present in soil affects root physiologic processes.

A.2. Effect of mycorrhizae

Mycorrhizae have a marked effect on root metabolism, affecting both nutrient and water uptake. Several studies (Heilman and Ekvan 1980, Ojala and Jarrell 1980) have shown that *Pseudotsuga menziesii* seedlings with more extensive mycorrhizal development were less responsive to phosphorous fertilizers. Such results illustrate how the development of infected roots related to healthy P status in the plant. Mycorrhizal plants had a greater dry weight percentage of P in the shoots than non-mycorrhizal plants and a high incidence of mycorrhizal infection in fine roots was often translated into greater leaf area and increased dry weight. Shultz and Kormonik (1982) agreed that non-inoculated hardwood tree seedlings were generally smaller, although they also had higher N, K, Ca and Mg concentrations and lower P levels. High cation concentrations in shoots and leaves of small-sized non-inoculated plants was attributed to a lack of ion dilution, possibly proving that, in some cases, mycorrhizae stimulated growth in addition to enhancing P uptake.

The advantageous symbiosis between plant and fungus does not exist in all conditions. Increases in N and P levels by fertilization have been shown to limit infection (Brix and van den Driessche 1974), likely because of the plants' lessened dependence on mycelia to search out these nutrients. Hydroponic studies by Wilde (1954) revealed that the surface area of roots free fron symbiotic organisms had no effect on the ability of seedlings to utilize nutrients; that is, if nutrient limitations are eliminated, so too is the need for mycorrhizae. Wilde also observed that the fungi are killed by prolonged water saturation. Fungal associations which effectively increase root surfaces are most likely to be present in well-drained sites.

The contribution of mycorrhizae to nutrient cycling has been quantified by Fogel and Hunt (1983). These fungi accounted for 6% of the total tree biomass in a *Pseudotsuga menziesii* ecosystem and together with roots, had larger stocks of all nutrients, except Ca, than the forest floor. Mycorrhizae alone accounted for the return of three times more N, P, and K than roots and equalled roots in return of Ca. Seventy three percent of net primary production was used for the growth and maintainance of roots and mycorrhizae. Nutrient cycling was

enhanced by the intimate association of fungi with tree roots; they may total only 2% of the ecosystem standing organic matter (Fogel and Hunt 1983), yet mycorrhizae are crucial in maintaining the fertility status of the system, and the nutrient status of the plant. Rovira and Bowen (1971), reviewing the effects of ectotrophic mycorrhizae which infect short lateral roots of *Pinus radiata*, noted such fungi have a high affinity for P and transport it between the cortical cells of roots. Mycorrhizal fungi may suppress root hair formation, yet effectively increase the surface area for uptake. This ia achieved by root radius increases from fungal-produced auxins and cytokinins altering root metabolism.

A.3. Effect of pH

The availability of many soil nutrients is strongly dependent on soil pH, with marked changes in solubility and ionic forms along a pH gradient. Levels of elements in plants grown under several pH levels reflect the differences in availability. Boron for instance, is more soluble and hence has higher levels in plants grown in soils of pH 5.0 to 5.4. than in plants grown in more alkaline soils (Gupta and MacLeod 1981). Phosphorous behaves similarly while Ca shows a reverse trend, becoming deficient in some species grown at pH 3.5 or lower (Ingestad 1979b).

Metallic ion content is directly related to soil pH (Kinzel 1983). In acidic soils, Fe^{2+} and Mn^{2+} are most soluble, sometimes reaching toxic amounts. These acidic cations and others such as Al^{3+} are nearly non-existent above pH 5. Molybdenum, absorbed as the anion MoO_4^{2-} is less available under acidic conditions. One may expect the appearance of Fe deficiency symptoms in alkaline soils, whereas in acidic soils the adverse effects of Al on DNA synthesis and carbohydrate metabolism produces roots with abnormal morphologic and physiologic features.

In Ingestad's work (1979b) with nutrient solutions, the rate of NO_3^- uptake was found to decrease with pH while NH_4^+ increased. The result was a nitrogen content apparently independent of pH. Similarly, P and K dry weight concentrations remained constant as pH

varied. In contrast, Ca and Mg concentrations in *Betula verrucosa* seedlings increased on a dry weight basis with increasing pH. Ingestad suggested that nutrient content on a dry weight basis is more informative than using fresh weights because on a fresh weight basis, uptake may appear to be independent of pH.

As soil pH affects nutrient solubility, it also influences soil microorganisms and their role in nutrient cycling. Lime additions, by raising pH and Ca content, may alter nitrification and the subsequent mobility of soil N (van Lear 1980). Fungal associations of *Pinus radiata* are inhibited by alkaline conditions (Theodorou and Bowen 1969), so that the nutrient turnover rates and plant productivity are also pH dependent. For all plants, there is an optimum value of soil pH - a balance of nutrients where levels of availability and solubility are neither toxic nor deficient.

Climatic factors, like soil factors, may have a defined optimum for a particular species at a particular stage of development. Observed effects of light intensity and soil temperature on dry matter production, for instance, illustrate that growth is maximized in a particular climatic range (Brix 1972). The effect may be mediated by root respiration which is temperature dependent (Ingestad 1979b), involving ion uptake and nucleic acid metabolism.

The abundance of research dealing with climatic and pedologic factors governing plant development and metabolism is an indication of the complexity of floral physiology. In this regard, soil fertility, mycorrhizae and pH have been extensively reviewed in such publications as those by Rorison (1969), Samish (1971), Mortvedt (1972), Carson (1974), Brouwer *et al* (1980), Atkinson (1983) and Tinker (1984). These topics were subjected to a scant overview here and were included only to introduce some basic principles which may be involved in the progeny tests conducted here.

B. GENETIC THEORY

B.1. Heritability

Although individual plants may display a preference for a narrow range of pedologic and climatologic parameters, the species may be present naturally over a wide range of values for these parameters. A wide range of occurrences is often accompanied by a degree of tolerance built up to withstand sub-optimal and supra-optimal conditions, conditions which can induce stress in the form of nutrient toxicity and deficiency, temperature extremes, salinity and water stress. The resultant selection pressure exerted on the species over successive generations eventually causes the evolution of specific adaptive features. Even such biotic effects as competition and alleopathic reactions may be implicated in the evolution of a growth habit for successful regeneration and reproduction (Eis 1981).

The more restricted in distribution the less flexible a species would be in terms of physiologic abilities (Ingestad 1979c). If maximum growth rate is achieved under widely varying nutrient regimes, then effective adaptive mechanisms may produce good growth and high competitive ability under these regimes.

Brown *et al* (1972) listed 5 steps in the evolutionary process:

1. mutations furnish variation,
2. sexual reproduction produces many gene patterns,
3. certain gene patterns provide greater fitness in the environments available,
4. natural selection increases the frequency of adaptively superior gene patterns, and
5. groups of gene combinations of adaptive worth become segregated into a closed system.

The end result is a broadly occurring species with physiologic heterogeneity. The selection pressure of the local habitat will effectively screen the population for individuals or genotypes whose behavior and traits are most advantageous.

Plant breeders interested in disease resistance, stress tolerance or some other economically important trait under strong genetic control will often measure the relative importance of these two factors using randomized and replicated tests and will select individuals from a wide genetic base. Samual and Johnstone (1979) agreed that reliable estimates of variation and descriptions of patterns of inheritance of desired characters are a necessary prerequisite for the success of breeding strategies.

In the past, many breeding programs, including those for cereal crops, have developed varieties for maximum yield in favorable environments, with sufficient phenotypic stability so as to be capable of exploiting environments improved by fertilization or site preparation (Finlay and Wilkinson 1963). With respect to trees, an ideal genotype will sustain growth at low substrate levels and respond positively to higher substrate levels (Jahroni *et al* 1976). These will have superior dry matter production via efficient absorption of nutrients.

For conifers, selection is the method preferred over inbreeding, hybridization and mutation breeding. Selection is carried out among geographic regions, among stands within regions and among trees within stands (Morgenstern *et al* 1975). This allows one to elucidate the heirarchial levels of variation patterned within forest tree species. Most northern conifers have an enormously variable genetic base, necessitating extensive range-wide testing of provenances to determine the patterns and quantity of variation. Provenances are often evaluated in tests which may fulfill one or more of the following goals (Fowler 1979):

1. determination of the best seed source for reforestation,
2. determination of overall pattern of genetic variation and to relate this to environmental factors, and
3. obtain a genetically variable collection of materials for further selection and breeding.

The genetic homeostasis of a population, a measure of stability reflected in the ability to adjust to fluctuating environments, is quantified in terms of the variability observed within a population grown in one environment (Hanson 1970). Provenance tests can reveal the relative

genetic stabilites of populations from their capacity to respond to the stresses imposed by different environments. Varietal yields , regressed on an environmental basis, can show which populations perform better in unfavorable than in favorable environments.

A second tool for tree breeders searching for second and third generation material is progeny testing with designs to evaluate the ability of stand members to produce superior offspring (Wright 1975). Illustrating this, Ying and Morgenstern (1979) showed that 17-year growth of progenies of selected *Picea glauca* plus-trees was not significantly different than those of randomly selected trees. The test of offspring of members of a provenance enabled the researchers to conclude phenotypic selection for height growth was ineffective.

Isolation of potentially superior trees is beset with numerous problems:

1. inbreeding,
2. differences between traits in the degree of genetic control,
3. differences in the response curves of traits, and
4. changes in the genetic expression of traits with age.

These points should be considered in addressing the nature of genetic improvements in cultivated plants.

B.2. Inbreeding

The extent of inbreeding in natural stands confuses the interpretation of genetic gains by selection as the reproductive union of genetically related individuals often causes a phenotypic depression. The amount of inbreeding is determined by distance and rate at which genes migrate within or between stands. Effective pollen movement is predominantly short-distanced; over 75% of all pollen normally remains within 100 m of the source. There are no barriers to self-pollination or fertilization and hence, there is often a high degree of relatedness or inbreeding among neighboring trees. Inbreeding depression may result, marked by a reduction in seed set, germination capacity, vigor and deformed growth (Mergen *et al* 1965). Homozygous lethal recessive loci, produced by self-fertilization, likely cause the

observed inferiority. Non-lethal homozygous recessive traits, being disadvantageous, may produce less than average performance.

Coles and Fowler (1976) cautioned that superior growth of progenies from a seed orchard may be considered a genetic improvement of stock, however, it may merely represent a reduction in the amount of inbreeding as there are more unrelated trees in a orchard than in a natural stand. The success of plus-tree selection programs - the selection of superior field performers - may be inhibited by the degree of inbreeding, as ordinary trees may just be more inbred, not carriers of inferior genes (Khalil 1975, 1978).

B.3. Degree of genetic control

The phenotypic expression of quantitative traits is governed by the environment and a myriad of genes, each with a specific function. By definition, heritability refers to the proportion of the total variation in a trait that is determined by genetic factors (Morgenstern 1974); the balance of phenotypic expression is mediated by the environment. Therefore, heritability estimates for different traits will reflect the degree of genetic control. Such estimates assume that environmental influences remain constant.

Based on parental performance, a highly heritable trait such as date of flushing would be a predictable attribute of progeny and in a test plot, the strong parent-progeny correlation may be independent of microsite influences and competition (Morgenstern 1976). By comparison, height growth variation often displays greater dependence on numerous physical, chemical and climatic factors, i.e., the trait has less genetic control. Here, genetic gains would be difficult to predict as progeny performance may not reflect parental yield.

The use of clonal material in field tests separates environmental from genetic components (Morgenstern 1974). With fixed genotypes observed variation can be attributed to the environment. Monitoring the stability of the various traits along environmental gradients would reveal the extent to which the traits are affected by environments and allows researchers to infer the degree of genetic control for that trait. It is important that selection programs

simulate outplanting conditions so that the results can be used to anticipate the morphologic and physiologic behavior of the material in field situations.

Hanson (1970) stated that two genotypes may have unique relative genotypic stability— the capacity to adjust to stress in different environments, usually measured by regressing varietal yields on an environmental basis. Stability may be a unique characteristic of a genotype; each genotype can be distinctly different in terms of response to environmental stress. Similarly, two different traits may respond differently to the same environmental stress. In a breeding program, it becomes inherently difficult to exclude traits with different response curves or negative correlations to each other; it may not be possible to maximize all of the desired traits using any one environment. Traits may have overlapping response curves according to natural selection and co-evolution, yet the regions of sub- and supra-optimal values may differ (Knight 1973).

B.4. Response curves of traits

Earlier reports list the traits known to be positively correlated, i.e. rising and falling in the same portions of a physical or chemical gradient. Bell *et al* (1979) reported that height, dry weight, and shoot:root ratio are positively correlated both phenotypically and genotypically, therefore artificial selection for one trait would result in a positive response of the others. Jahroni *et al* (1976) showed that total nutrient accumulation was positively correlated with growth, perhaps because larger seedlings have more roots and hence a larger capacity for uptake. The model of trait relatedness is confused by negative correlation in this case between diameter growth and nutrient accumulation and between height and diameter. They concluded the genes affecting accumulation and distribution of nutrients or height growth were not the same as those affecting diameter growth.

B.5. Changes in expression with age

One final problem in the evaluation and control of plant performance is the change of genetic expression with age. Namkoong *et al* (1972) cautioned that seedling height differences in *Pseudotsuga menziesii* may have no effect on eventual population differences, i.e. performance ranking of provenances may be subject to age-related variation. Genetic control of apical growth tends to decline past the juvenile years. Several growth strategies may appear within a population, including one which maximizes early growth and one that limits response to environment and allows constant growth. Once in the dominant stage, height growth becomes more uniform and within population genetic differences are reduced. Seed size effects are apparent early in seedling establishment and eventually diminish, showing no significant correlation beyond 10 weeks of age in *Pinus taeda* (Waxler and van Buijtenen 1981). In other findings, some aspects of seedling performance may be well correlated to 8-year volumes (Cannell *et al* 1978); however, the correlations weakened when extended to mature-tree characteristics. In Cannell's work, date of bud set, water stress response and root:shoot ratio were the features monitored.

If progeny tests indicate there are family effects for measured parameters then the parameters are said to be under genetic control. This implies that the mother tree, the tree from which seeds were collected, has passed on some properties or heritable traits to its progeny. In forestry research, family effects have been observed for many metabolic responses to environment, including the ability to efficiently utilize fertilizer-nitrogen (Bell *et al* 1979) or fertilizer-phosphorous (Walker and Hatcher 1965, Jahroni *et al* 1976).

The degree of genetic control, termed heritability, is often a major condition on which selection is founded. Genetic gain is the heritable difference in growth of selected progenies relative to the entire population assuming the progenies and the populations are normally distributed with respect to the growth parameters measured (Teich and Khalil 1973). As Foster and Lester (1983) stated, if some of the total variation is due to differences among families there is potential for genetic gain.

A heritability component can arise from the determination of such morphologic features as height growth, dry weight, and shoot:root ratio (Waxler and van Buijtenen 1981). These workers found shoot:root ratio and shoot weight were different between fast-growing and slow-growing families. There was little variation in root weight among families, therefore most family differences are due to shoot weight. Cannell *et al* (1978) disagreed, saying rooting habit may be used to differentiate families. In their tests, families producing the greatest 8-year volumes grew fastest under mild stress and these families tended to have low shoot:root ratios and relative growth rates, suggesting that superior volume producers avoided water stress by developing more extensive root systems. Such anatomic characters as seed weight and cotyledon number also have a strong genetic basis of control (Meagher 1976).

The heritability of family means for height growth has been estimated as high as 0.57 (Foster and Lester 1983). Kuser and Ching (1981) found that family variation averaged up to one half of the provenance variation for most growth responses of greenhouse-grown *Tsuga heterophylla* seedlings. In some cases, a species may be structured with most of the variation occurring as family effects. Wheeler and Guries (1982) calculated that 91% of allozyme variability in *Pinus contorta* resided within populations whereas the remainder was distributed among populations. Based on interpretations of patterns of allelic frequency, Yeh and O'Malley (1980) stated that 97% of the total diversity in *Pseudotsuga menziesii* resided within populations. While allozyme variation is not an accurate reflection of environment-induced differentiation, such results supported Meagher's (1976) claim that heterogeneity found among open-pollinated families is at least partially caused by the seed parent (mother tree). Controlled crosses have shown the influence of the male parent in determining growth capabilities is also significant (Jahroni *et al* 1976).

Family effects are not always definitive. In an examination of *Picea mariana* progeny on wet and dry sites, Morgenstern (1974) found that progeny-parent correlations were not significant, as only 18% of the total height variation was genetically controlled. Hence, mother tree growth was not a useful predictor of progeny growth. The strength of environmental

influence has diminished apparent genetic effects. A similar case was observed with glasshouse-grown *Picea sitchensis*. The cause was attributed to the inability of juvenile assessments to reflect adult family performance (Samual and Johnstone 1979).

B.6. Provenance effects

Many factors prevent the direct extrapolation of glasshouse results to field trials. Glasshouse trials may reveal whether or not nutrient deficienies exist in the soil, but they may not indicate the level of a particular element required at maturity. Juvenile-mature correlations are often low, preventing extrapolation of early results to adult harvest (Morrison 1974). The use of seedlings may be warranted, however, as the accelerated growth under optimal climatic conditions allows for early evaluation of progeny and provenances (Wood and Hanover 1981). To the argument that controlled environment facilities are unnatural, Ledig (1970) countered that field tests , usually subject to some site preparation, are equally unnatural and less easily duplicated. Finally, Furlani *et al* (1984) added that controlled environments are an inexpensive alternative to laborious field screenings. By enabling precise controls to be placed on some parameters to observe the response of seedlings to specific influences, conditions may be varied to maximize or minimize differences in genetic expression (Mergen and Worrall 1965).

Wright (1975) cited the example of a progeny test where 25% and 75% of the total genetic variance was due to differences among and within families, respectively. Several researchers have monitored the performance of seedlings from numerous provenances of northern conifers. Khalil and Douglas (1979) and Kuser and Ching (1981) examined *Picea mariana* and *Tsuga heterophylla*, respectively and found the responses to be geographic location-dependent. There was a relationship between geographic origin and the varietal adaptations of the trees. Progeny height was expressed as a function of latitude, altitude, frost-free days, temperature, precipitation and mean July daylength. In combination, these influences contributed to the existence of the provenances, each with a unique response pattern to the conditions imposed. Strong latitudinal and elevational clines were found, with seedlings

of southern or coastal provenances growing faster.

In other work, the physical parameter responsible for the patterns of evolution have been identified. Elevation-induced inherited population differences in growth rate have been found in *Pseudotsuga menziesii* (Namkoong *et al* 1972) and in *Acer saccharum* (Wood and Hanover 1981). Rehfeldt (1983) related 86% of the variance among populations of *Pinus contorta* to latitudinal differences in seed source origin.

To explain within-species heterogeneity, Meagher (1976) hypothesized that there is gene exchange along climatic gradients and the intense selection pressure of the local habitats alter the allelic frequencies of the breeding population. The argument for genetic uniqueness among provenances was supported by Miksche (1968), who studied the DNA content of 17 seed sources of *Picea glauca* in Canada. DNA concentration per root tip cell was correlated to latitude and longitude. Since DNA content determines the length of mitotic cell cycles, the growth response differences could be explained in terms of histochemical differences. Physiologic variation leading to anatomical differences are thought to mediate the apparent differences among provenances.

Pollard (1973) noted different phenological adaptations of the apical meristem to deteriorating environmental conditions in the autumn in several *Picea glauca* provenances. Development of a large number of needle primordia depends on the ability to prolong needle initiation, a process affected by latitude and the length of the frost-free period. Slow-growing provenances, composed of genotypes that do not continue primordia production after early September, may predominate at higher latitudes. Pollard quantified the effect in *Picea sitchensis* noting that southern provenances from Oregon may produce as many as 35% more needle primordia than those from Alaska. Date of flushing and length of dormancy are other adaptive characteristics engrained in populations from different ecological zones (Roche *et al* 1969).

C. G X E INTERACTIONS

The interplay between environment and genotype results in a characteristic phenotype of an individual. When provenances are tested in different environments, interactions between population genetic effects and environmental effects are reflected in differences in response to the environments (Mergen *et al* 1974), i.e., differential ranking of populations across the environmental gradient. This represents the third component contributing to the phenotypic expression of an individual, an expression commonly written as:

$$P = G + E + (G \times E)$$

According to Snaydon (1962), a widely occurring species may be composed of individuals having broad physiologic tolerance or of genetically distinct 'sub-species', each adapted to a narrow range of conditions.

Gene exchange occurs continously along elevational and latitudinal gradients (Meagher 1976) with physiologic types within a species grading into one another (Campbell and Sorenson 1978, Dunsworth and Dancik 1983). Spatially separated seed sources would be discrete members of a clinally-structured population. If seedlings, sampled to represent this variability, are planted on sufficiently varied environmental conditions, the presence of a provenance X environment interaction implies either the ranking of population samples or the relative magnitude of differences between population samples is not identical in all test environments. The interaction is measured as the differential response of the phenotypes to the environments, that is, by the failure of a difference between populations to be the same in two environments.

Table II.1 depicts a G X E interaction, such as those elucidated from provenance tests.

Table II.1. Sample illustation of a genotype x environment interaction. Results from a hypothetical provenance test.

		ENVIRONMENT		
		1	2	3
GENOTYPE	A	10	25	30
	B	15	20	35
	C	20	30	40

In this table, all genotypes are responding with an increase in an arbitrary trait across an environmental gradient (from *E1* to *E3*). In *E1*, genotype A ('*gA*') ranked below *gB*; the same was found in *E3*. However, in *E2* the ranking is reversed, indicating the presence of an interaction. Relative to *gB*, *gA* was particularly favored in *E2*. Significant changes in the rank of genetic entities is more important in the evaluation of interactions than instances in which populations display a constant relative superiority (Squillace 1970), as in the performance of *gC*, which ranked above its counterparts in all test conditions.

When interactions are significant in an analysis of variance, clines can be described by stepwise multiple regression of population responses in relation to elevation, latitude, soil fertility or whatever other parameter the researcher uses in selecting provenances (Campbell and Sorenson 1978).

Using provenance tests, one can estimate environmental ranges within which populations are physiologically attuned (Rehfeldt 1983). Interactions are considered strong if plants from different places retain their morphologic and physiologic distinctions when grown together in a common environment (Goodman 1969). In such a case, ecotypes may be confirmed to exist and the information incorporated into practical breeding programs where separate strains are developed for specific environments. If interactions are faint, one strain may be used for all outplanting sites. Thus knowledge of the magnitude of G X E interactions helps foresters decide the need for separating seed sources, thus avoiding the bias occurring in

estimates of genetic gain when interactions are not considered (Squillace 1970). Breeding programs have as an objective, the minimization of G X E interactions in each location, so that uniformity and superiority of trees can be attained; all individuals in a field site will be superior in performance to the wild population from which the selections were made. Useful genetic variance is increased by reducing the variance component for G X E interactions in the homogenous population developed for a given environment (Campbell and Sorenson 1978). Foresters testing diverse provenances from natural populations can isolate desirable genotypes for any one environment, thus lowering the relative magnitude of the interaction in each outplanted population (King 1965a). Selection of specific populations of individuals suited to certain conditions ensures a genetically superior stand will result in outplanting operations.

When interactions are strong in non-selected populations, researchers often search for any patterns in variation existing with respect to quantifiable environmental factors. This would facilitate practical application of seed zonation. The potential success of various selection strategies could be predicted if biological explanations were available. Summarizing their utility, Fowler (1979) listed three uses of provenance tests:

1. determination of the best seed source for use in reforestation,
2. determination of the overall pattern of variation and to relate this to environmental papameters, and
3. obtain a genetically variable collection of material for future study and breeding schemes.

No design satisfies all objectives; budget, time or resource restraints require a compromise of objectives in most tests. Still, they often have as a goal, the identification of best provenances on a broad regional basis, more rarely on a small stand level. Genetic variation is not completely clinal, therefore it is often hard to identify the best seed sources using several ideal criteria. Nature's idea of best adapted is being able to tramsmit genes, while man's idea of the same is usually being able to have the biggest volume (Fowler 1979). When dealing with northern conifers, the large amount of within-stand variation as well as between-stand

variation requires that numerous populations be sampled and high numbers of seedlings be grown in tests to resolve G X E interactions.

While most natural adaptive responses are derived by a wide range of climatic and pedologic factors, most studies can practically deal with only one or two parameters. In numerous citations, G X E interactions have been causally related to indentifiable environmental factors.

In the section to follow, genotypic response to soil microbiological and chemical parameters will be reviewed, as the intent in this project was to resolve intraspecies diversity in relation to these gradients. It is acknowledged that physical properties such as texture differed between regions and hence could have been the basis for differentiation. Restrictions on technical and financial resources necessitated a focus on the few soil factors described.

C.1. Effects of soil fertility

The occurrence of G X E interactions has been attributed to many soil factors. Some documents pointed to physical effects, as in a report where depth and permeability of soils had a controlling effect on rooting pattern and caused ecotypic variation in *Picea glauca* and *Pinus contorta* (Eis 1970). A review by Popp (1984) paid attention to soil chemical regimes, relating growth differences in plants to nutritional adaptations. Investigations of wild plants from extreme habitats revealed great variablity in mineral metabolism and unique varietal properties of uptake selectivity in cultivated plants. As examples halophytes, metallophytes, calcicoles and calcifuges exist as physiologic ecotypes by virtue of their mineral metabolism characteristics which in turn mediate elemental contents and morphologic features.

Woolhouse (1969) hypothesized that the chemical environment of the soil is a dominant component in the selection complex, acting on plant populations because of the intimacy between the plant and soil. At membrane surfaces, the direct confrontation between structural and catalytic proteins and the chemical environment may affect enzymatic roles and ion transport carriers. Such effects at the root-soil boundary (rhizoplane) elicit a more rapid

response in plant metabolism than climatic effects, which may be buffered over time by overstory vegetation or micro-topographic position.

Calcium

Of the ions exerting an influence on genetic divergence, calcium is one of the most well researched. Typical of the work to explain genetic differentiation in terms of ion selectivity, Waquant and Bouab (1984) monitored foliar nutrient levels in specimens from transplant experiments. On acid soils, plants from a calcareous soil accumulated more Ca and less K than plants from acidic soils. On calcareous soils, the response was reversed; acid-originating plants contained more K and less Ca. Similar responses to calcium are hypothesized to have differentiated *Picea glauca* populations in Ontario into edaphic ecotypes (Farrar and Nicholson 1967, Teich and Holst 1974). Progeny from high-calcium limestone soils and from low-calcium granitic soils grew best with parental soil conditions. Provenances of *Fagus silvatica* reacted to substrate pH and calcium levels, giving rise to interactions as monitored in terms of root collar diameter and height growth (DuCros and LePoutre 1983). Morphologic leaf characters such as average length and total weight exhibited a significant degree of substrate-induced variation, as did foliar Ca, Mg, P and K levels.

Differential calcium requirements were discussed by Foy (1974) who cautioned that it is difficult to determine which of the physiologic factors that are correlated with tolerance to soil conditions are causally related to plant adaptation. Acidic soils of limiting calcium content may have toxic levels of Al or Mn so that calcifuges, plants from acidic low Ca soils may also possess tolerance to Al in addition to tolerance of hydrogen ions. Calcifuges are usually characterized by low calcium uptake, high K:Ca ratios in tissue and slow growth rates, whereas calcifuges from calcareous habits are distinguished by differences in Ca uptake and translocation rates (Foy 1974a). They commonly have more efficient absorption of K and prefer K uptake over Ca, an ion selectivity which may distinguish the ecotypes. Clark (1983) agreed that the accumulation of Ca is heritable. He found some genotypes capable of producing more dry matter per plant and more dry matter per unit amount of Ca, with fewer

Ca deficiency or toxicity symptoms at low and high Ca levels; these were termed 'Ca-efficient'. Growth on calcareous soils may be assisted by compensation mechanisms built into root metabolic activities, as Woolhouse (1969) cited evidence for growth on such soils to be related to organic acid metabolism in response to carbonates. Plant tolerance to high pH soils may be mediated by increased production and exudation of citrate and other low molecular weight organic acids which serve to decrease the pH of the rhizosphere.

PH

A provenance test conducted by Pope (1982) suggested some *Platinus occidentalis* families may have greater biomass accumulation and nutrient upatake than others at certain pH values. Kinzel (1983) hypothesized that differences between acidophilic and basophilic varieties may be based on hydrogen ion exclusion by adapted root tissue or specially constructed cytoplasmic membranes. In acidic soils, however, it may not be the H^+ that is toxic, rather increased Fe and Al solubilities may contribute to the adverse conditions. It was these ions that most workers claimed the plant reacted to under acidic conditions (Foy 1974a, Clark 1983).

Aluminum

Aluminum inhibits proper root elongation due to chromosomal irregularities in mitotic migration (Foy 1974b, Steiner and McCormick 1980, Kinzel 1983). In the nucleus, the element forms crosslinkages with phosphate groups, making DNA abnormally rigid. It also crosslinks protein molecules and pectins in the middle lamella, thereby increasing protoplasm viscosity and decreasing overall permeability of salts. A reduction in Ca and P uptake results. Differential Al tolerance to such adverse effects can take several forms, as outlined below:

1. tolerance by resisting morphological damage and continuing root elongation. In one grass species, Levitt (1972) found resistence was due to the accumulation of the toxic ion in root cell walls, thus avoiding stress by keeping the ion away from the protoplasm. Active exclusion could occur via exclusion pumps as well.
2. tolerance by raising the rhizosphere pH, thus decreasing Al solubility. Brown *et al*

(1972) documented an increase in solution pH caused by Al-tolerant varieties of wheat. Here, it is possible that Al-resistant plants exude hydroxyl ions at the root surface which precipitates the Al as $(Al(OH)_3)n$. Sensitive varieties lacked this ability (McLean 1976).

Clarkson (1969), Levitt (1972) and Foy (1974b) examined ion stress avoidance, compiling a list of possible mechanisms by which this may occur:

1. ion dilution relying on the plastic extensibility of cell walls.
2. tolerance through lower root CEC and less Al accumulating in roots, *i.e.* exclusion via low ion permeability.
3. tolerance by becoming less susceptable to Ca deficiency, i.e. becoming more Ca-efficient.
4. secretion of excess absorbed ions into vacuole, where they remain isolated from aluminum-sensitive proteins and phosphorylated compounds.
5. tolerance by developing greater affinites for Mg and K.
6. tolerance by the production of organic acids in roots to prevent internal precipitation of aluminum phosphates, increasing P transport to shoots, while retaining less P in roots.

Aluminum-tolerant plants have alterations in the structure and function of 'ATPase' to enhance P absorption and utilization and root respiration in the presence of excess aluminum (Clarkson 1969, Brown *et al* 1972). Examining lead spoil- and calcareous-grown races of *Agrostis tenuis* and *Festuca ovina*, Woolhouse (1969) found that increased Al concentations caused decreases in ATPase activity in three races. The decreases were greatest in calcareous races and least in those from lead spoils. It is possible that genotypic differentiation existed with ecotypes developing Al tolerance along one or more of these means.

Iron

Plant genotypes differ in their abilities to absorb and translocate iron. Calcareous-habitat plants may exhibit Fe-efficiency by the ability of roots to alter the rhizosphere environment (Brown *et al* 1972, Clark 1983). The means of achieving this include:

1. excreting H ions to lower pH and increase Fe solubility.
2. excreting compounds to reduce iron, thereby making the rhizosphere Fe more available.
3. increasing the rate of reduction of iron in roots.
4. increasing root organic acid production, especially citrate, which prevents the precipitation of Fe by phosphates. Chelated iron is then tranported via xylem throughout the plant.

Phosphorous

Woolhouse (1969) and Clark (1983) claimed that some genotypes were unique in their ability to compete for P and in the activity of root phosphatases, representing differences in the ability to utilize organo-phosphates in the soil. Phosphate-effecient plant genotypes had lower shoot:root ratios of P and higher dry matter accumulated per unit of P.

Nitrogen

In several instances, the influence of soil nitrogen levels are implicated in G X E interactions. Five *Pinus elliotti* provenances, in a test to evaluate ion absorption and utilization, showed significant fertilizer X provenance interactions for N and K concentrations of stems and needles (Walker and Hatcher 1965). Plant part weights also showed distinct variability, with the ranking of progeny groups dependent on fertilizer- nitrogen treatment. Again, some anatomical features such as mean needle length, in this case, were not affected. Nevertheless as with previous citations, physiologic differences among provenances had been demonstrated. Namkoong *et al* (1979) and Bell *et al* (1979), using *Pseudotsuga menziesii* and *Pinus taeda* respectively, found similar family effects on 10 to 20-year height and diameter growth in the interaction of provenances with N fertilizer. These traits were positively correlated both phenotypically and genotypically, an added benefit to tree breeders, who by selecting one trait, would find genetic gains in others as well. In one study by Mergen and Worrall (1965), latitudinal differences in *Pinus banksiana* provenances were reflected in chlorophyll content of needles and needle color. The mechanism of N responses may be traced

to the uptake and assimilation of nitrogen (Clark 1983). In this regard, genotypic differences may be due to differences in nitrate reductase, resulting in variable protein levels of seed and foliage.

C.2. Climatic effects

Climatic gradients along a continuous geographic range have been well documented to be responsible for ecotypic variation. Elevation, for instance, has been shown to account for 86% of the variation among *Pinus contorta* populations (Rehfeldt 1983) when multiple regression models were used to relate adaptive differentiation to geographic and ecologic characters of 28 seed sources planted in three environments. Noting soil temperature decreases with elevation, Higgins and Spomer (1976) detected differences in temperature optima for root respiration in several grass and herb species. Alpine provenances had adapted higher root respiration levels for an increase in competitive edge in alpine habitats. The same plants were mal-adapted to warmer conditions where such metabolic rates would be wasteful. This effect of altitude on respiration rates may extend to affect mineral absorption, accumulation and assimilation strategy. In another study, height growth, needle length and needle color were all demonstrated to vary according to the geographic origin of the *Pinus silvestris* seed (Steinbeck 1966). Seeds collected from around Europe and planted throughout the United States exhibited seed lot X site interactions with respect to magnesium, cobalt and aluminum contents and in addition, there were anatomical differences among the seeds of diverse origin.

Altitudinal and latitudinal clines are often cited together as seedlings respond similarly to the gradients. Examples of such seed source response to warming temperatures in spring and declining daylength in autumn have been observed in *Picea rubens* (Roche 1969, Morgenstern 1976) and in *Tsuga heterophylla* (Meagher 1976). Data of flushing and bud formation were among the traits monitored to establish this relationship. Northern and high-altitude sources showed earlier growth cessation and tended to flush earlier than others. In *Pinus elliotti*, the variation in time of bud burst could be as much as 3 weeks (Bengston *et al* 1976).

With *Picea glauca*, Pollard (1973) confirmed that latitudinal differences, as affecting frost-free period resulted in provenances with varying abilities to prolong needle initiation. Northern provenances had fewer needle primordia as a result of the phenological adaptations of the apical meristem to deteriorating conditions in the autumn. Pollard (1975) further elaborated that northern sources of *Picea sitchensis* were faster growers during the first 12 weeks after flushing, when needle primordia are initiated and shoot elongation occurs, however these provenances were the first to cease when photoperiod declined. In southern sources which had slower accumulation of primordia the activity persisted longer, eventually to surpass those of the northern sources.

Morgenstern (1976) stressed the importance of such adaptations in delineating seed zones. Provenances from low latitudes and altitudes respond more slowly to warming temperatures in the spring and declining daylengths in autumn than do other seed sources. High altitude sources grown at low altitudes may flush too early, when snow is still covering the low areas. Therefore frost damage may then occur in seedlings displaced into foreign environments.

Displacement into different photoperiod regimes may also affect the timing of growth cessation, as when northern sources grown in southern areas never experience the long days they are adapted to. According to Morgenstern, they may develop buds after June 21 even though there is a longer growing season available. Dunsworth and Dancik (1983) found significant among-source variation in a *Picea glauca* provenance test. Northern Alberta sources had higher above-ground and total relative dry matter than other sources in two simulated climates, while sources from central and north-central Alberta had more branches. In their work, elevation-governed responses were masked by an apparently greater effect of photoperiod caused by displacement in latitude.

When *Pinus silvestris* provenances were planted at various sites and leaf length and color monitored, sources from the northern part of the range had longer needles at the southern plantations (King 1965b). The significant seed source X plantation interactions in needle

length were accompanied by similar trends with respect to needle color. Again, the parental climate may have engrained considerable effects on metabolic pathways for such results to occur.

Miksche (1968) hypothesized that seed source differences in *Picea glauca* and *Pinus contorta* may be attributed to the DNA content per cell. Seedling height was inversely proportional to DNA content per cell, as greater contents lengthened the mitotic cycle and caused slower growth. Miksche concluded that the selection of DNA content may be a means by which genetic factors influence growth rates.

C.3. Evaluating G X E interactions

Use of Seedlings to Study G X E Interactions

Early growth results are commonly used to describe genotype X environment interactions in tree species. Wood and Hanover (1981) claimed that marked differences between provenances and families of *Acer saccharum* were apparent in 4-month old seedlings subjected to conditions that accelerate growth; continous light, controlled temperature fluctuations and frequent fertilization were used. In a study of *Fagus silvatica*, DuCros and Lepoutre (1984) saw provenance differences in response to soil status in seedlings as early as 1 year after germination, by which time there were indications that parental substrate had exerted a selection pressure, causing apparent genetic differences among provenances.

To answer concern over a possible lack of a juvenile-mature correlation, Cannell *et al* (1978) found that the rate of seedling growth is influenced initially by differences in seed size until *Pinus taeda* seedlings were about 140 mm tall. Thereafter, 4 growth traits of well watered seedlings were stongly correlated with 8-year volumes on a family basis. The traits monitored were:

1. date of bud set,
2. seedling growth in response to seed weight,
3. water stress response, and

4. shoot:root ratio.

Meagher (1976) control-crossed *Tsuga heterophylla* individuals and observed family-related height influences at 6 months. From studies of seedling progeny, three facts were revealed:

1. there are differences in seedling phenology and growth between populations separated by small differences in altitude and latitude,
2. variation in seedling behavior may be attributed to the seed parent, and
3. these interpopulation differences between the cone parent are genetically based.

The value of early progeny selection was also supported by Teich and Khalil (1973). Genetic gain by selecting the tallest 10% of families of *Picea glauca* can be as high as 17% in 2-year old seedlings. Comparing this to a gain of 26% after 11 years, there were clear benefits in early selection.

Other workers have shown a greater reluctance to invest a large amount of confidence in early progeny test results. Bell *et al* (1979) identified family X nitrogen fertilizer interactions after one year in *Pseudotsuga menziesii*, but did not extrapolate their findings to possible adult responses. King (1965a) also stated it may be difficult to extrapolate to the adult stage, knowing there may be no relation between young and old responses. He testified that interactions might only develop as trees mature, as in a case of *Pinus sylvestris* showing no seed source X environment interactions at 7 years, although there was one at 20 years. Samuel and Johnstone (1979) found 6-year juvenile assessments of *Picea sitchensis* do not necessarily provide information on family performance later on.

By the existing contradictory evidence, it would seem that the strength of juvenile-mature correlations depends on the trait measured and its degree of genetic control. Waxler and van Buijtenen (1981) isolated the seedling growth parameters which were best predictors of field performance of the same *Pinus taeda* families. Shoot weight and shoot:root ratio were the best predictors of mature performance while seed weight differences and stem height correlations to parents diminished after 10 weeks. Initial height differences in *Pseudotsuga menziesii* have no effect on eventual population differences (Namkoong *et al*

1972). Population differences in height do not occur until about year 15, when interpopulation differences emerge and random site differences are reduced. Namkoong added that genetic control of apical growth is strongest in juveniles then declines with time, his explanation being that as trees grow into dominance, differences in growth among populations will be present and based on site productivity while genotypic diversity within populations is expressed less markedly. Therefore seedling establishment depends on rapid growth in a variety of habitats because of variation in habitat over short distances. Different growth patterns that may develop are dependent upon the degree of inbreeding and the competitive abilities of the individual. Hence, there may be an optimal strategy requiring genetic variation changes with age and population differences with age.

Parameters to Evaluate Seedlings

Seedling response to imposed treatments is often monitored on the basis of morphologic and anatomic features. As attention is directed to the effect of environmental conditions, the parameters should have some degree of manipulation from the environment. There should also be a component of genetic control, so that both factors may act interactively to control plant productivity.

Height growth is an acceptable parameter to measure in *Picea glauca* as it is strongly regulated by soil fertility, yet there is still a genetic influence since seedlings do not respond the same way under similar conditions (Armson 1966, Meagher 1976). Du Cros and Lepoutre (1983) illustrated the marked variability in height growth between *Fagus silvatica* provenances. Such characters as leaf weight or length showed little substrate-induced variation. Leaf size, they stressed, was under too much genetic control to be a sign of adaption. In one study, fertilization of white spruce field plots resulted in up to two times the number of secondary needles as non-treated seedlings, so number of needles could also be considered as a valuable measure of plant response to a treatment (Armson 1966).

As stated previously, there are numerous instances where early growth cannot be equated with adult performance (Namkoong *et al* 1972, Cannell *et al* 1978, Waxler and van

Buijtenen 1981). It is best to monitor seedling parameters that are strongly correlated to later performance. Cannell *et al* (1978) suggested shoot:root ratio be considered, as small differences in dry matter partitioning can have major effects on total plant growth. The degree to which seedlings invest assimilates into root production affects the seedling response to water or nutrient stresses (Cannell *et al* 1978). Ledig and Perry (1965) expressed the ratio of relative partitioning of biomass between shoots and roots as the coefficient K in the equation:

$$\text{LOG(shoot dry wt.)} = a + K \cdot \text{LOG(root dry wt.)}$$

Genotypes with high K values grow rapidly because they allocate a high proportion of assimilates into photosynthetic machinery, resulting in greater shoot heights and diameter under ideal conditions. If water or nutrients are limiting, genotypes with a low K grow faster as their more extensive rooting pattern permit greater water and nutrient uptake.

Two other environmentally-modified parameters are root dry weight and total branch length. For these Kuser and Ching (1981) cited an example of air and soil temperature affecting their expression in *Tsuga heterophylla* seedlings. The trend between seed source and treatment interactions was often vague, nevertheless the parameters were useful in revealing what relationships were present.

Ingestad (1970) advocated seedling assessment based on several temporally-spaced measurements. In his work with *Betula verrucosa*, he derived a rate of root weight increase, Δw, as follows:

$$\Delta w = \frac{\ln \frac{W_2}{W_1}}{t_2 - t_1}$$

where W_1 and W_2 are root weights at time t_1 and t_2, respectively. This is similar to a measure termed 'mean relative growth rate' used by van den Driessche (1968). Stem diameter has been proven unreliable as an indicator of vigor (Burdon 1971). In a test of clonal *Pinus radiata* material on various sites, Burdon noted that there was little repeatability between the clones of any one ramet at any one site. On sites of low productivity especially, stem diameter declined

and was considerably more variable than stem height. There may be a possibilty of interpreting stem diameter variabilty as a measure of site productivity potential, however this was not elaborated by Burdon.

Dunsworth and Dancik (1983) evaluated the performance of *Picea glauca* provenances in two simulated climatic regimes. The characters they assessed were height, diameter at first internode, number of branches and fresh and dry weights of roots and shoots, combined into several expressions of relative dry matter. They observed greatest variability among seed sources for number of branches. Relative dry matter as an approximation of hardiness increased as the latitude or elevation of the source increased.

Several researchers have devised a method of quantifying root responses to growth medium composition (McCormick and Steiner 1978, Steiner *et al* 1980, Furlani *et al* 1984). As an example, Steiner *et al* (1980) evaluated the response of *Betula papyrifera* families to 120 ppm Al and expressed their findings as a mean root tolerance index:

$$\text{Al tolerance index} = \frac{\text{root elongation with aluminum}}{\text{root elongation with no aluminum}}$$

The index removes the inherent variation within families in rates of root elongation.

External differences in trees may be accompanied by internal differences in mineral content (Mergen and Worrall 1965, Morrison 1974), hence foliar analysis is often informative in the diagnosis of factors influencing growth. Morrison advocated foliar sampling during the dormant period, when needlles are least likely to be affected by such confounding physiologic changes as growth dilution and luxury consumption. As expressions of mineral composition on a percent dry weight basis are confounded by seasonal changes in carbohydrate reserves, Smith *et al* (1981) suggested that it may be less erroneous to describe nutrient content per unit of leaf area. Using *Pinus banksiana*, Mergen and Worrall (1965) exemplified the effect of environment and seed source on foliar N, P and ash content. Between seed sources, differences in mineral content were attributed partly to varied abilities of seedlings to adapt to the soil environment.

Steiner *et al* (1980) noted that, with exposure to 120 ppm Al, the subsequent performance or degree of tolerance of provenances was reflected in the degree of foliar Al increases. The foliage content changes were attributed to reduced foliage growth on Al-injured plants since accumulations are expressed on a dry weight basis. The differences between tolerant and non-tolerant provenances were not consistent; however, mechanisms of Al toxicity could only be indirectly related to foliar nutrient concentrations. Du Cros and LePoutre (1983), devised the following expression to quantify the relationship between alkaline- and acidic-habitat levels:

$$Vr = \frac{(Xc - Xa)}{Xa}, \text{ where,}$$

Vr = relative variation in nutrient uptake between substrates.
Xc = uptake in calcareous habitats.
Xa = uptake in acidic habitats.

Calcium, Mg, P and K foliar levels were greater on alkaline habitats. Nitrogen, Cu, Fe and Zn levels showed no differences, hence were least applicable in describing provenance responses to substrates.

Researchers analyzing foliage should carefully ensure that water availability does not vary between fertility treatments. Many foliar characteristics are dependent on moisture stress (Leaf *et al* 1970). For instance, in water-stressed plants, percent ash and nitrogen and potassium concentration decreased, while magnesium levels increased.

Most research on nutrient uptake deals with the concentration of one element at a time, not accounting for nutrient interactions or ion ratios. For this reason, many workers feel it is more informative to analyze results using ratios of cations, (van den Driessche 1968, Braakhekke 1984).

Waquant and Boumb (1984) utilized triaxial diagrams to illustrate how the ability of plants to select ions is genetically different among provenances. Triaxial ratio diagrams were developed using the principle that two of the three possible ratios between elements would determine the third ratio. Coordination on two of the three axes lying on the same plane would be used to predict the coordinate of the third axis. Individuals differing in ion affinity are

separated by a measure of distance on the diagram and whole provenances can be seen to inhabit different regions (Figure II.1). An ion would commonly be expressed as a weight percentage of sulfur, which was not shown to have intraspecies differentiation. Braakhekke (1984) cautioned that such 'TD' diagrams are useful only when all components are of equal importance. He stated that their utility is realized when the relative importance of the three components is the same.

Sampling intensity is yet another consideration to be dealt with when foliage analysis is to reflect seedling physiology. Bergland *et al* (1976) stated that fertilizer or irrigation treatments increased the performance variability in *Pinus resinosa* plots. By inducing a higher level of heterogeneity, an increased number of samples were required to keep allowable errors at a certain level. For example, with allowable errors at ±10% of the mean and probability of a type I error at 0.05, the following sample sizes are needed for various characteristics (Figure II.2). Progeny tests performed in this project had considerations of the sample size-allowable error relationship. The experiments were conducted with physical layouts sufficiently large for the clear resolution of seed source and treatment means.

Use of Foliar Analysis

Like soil analysis, foliage analysis is essentially diagnostic; it enables researchers to identify factors influencing growth (Morrison 1974). Growth restrictions may be joined by visual symptoms and are used in solution cultures as a reference to the effect of induced deficiencies. Van den Driessche (1974) stated that foliar analysis had been inhibited in forest research by the high genetic variability of trees and the variability of forest soils.

Dominance class, crown position and needle age are sources of foliar variability and must be accounted for (Morrison 1974). Supressed trees often showed higher nutrient concentrations than dominant trees, but dominants had higher total nutrient concentrations on a mass per unit leaf weight basis. For most tree species, nitrogen is highest in current or year-old growth, P and K in current and Ca, Fe and Mn in older foliage (Morrison 1974). Nitrogen, P and K are depleted in older tissues and moved to growing regions. Magnesium and

Figure II.1. Example illustration depicting proportions of Ca, K and Mg % in shoots . Five 'G' plants and 5 'M' plants grown on their respective parental habitats (from Wacquant and Bouab 1984). The 'o' symbols indicate the position of each 'G' plant. The '□' symbols indicate the position of each 'M' plant. 'G' plants are from a calcareous habitat. 'M' plants are from an acidic habitat.

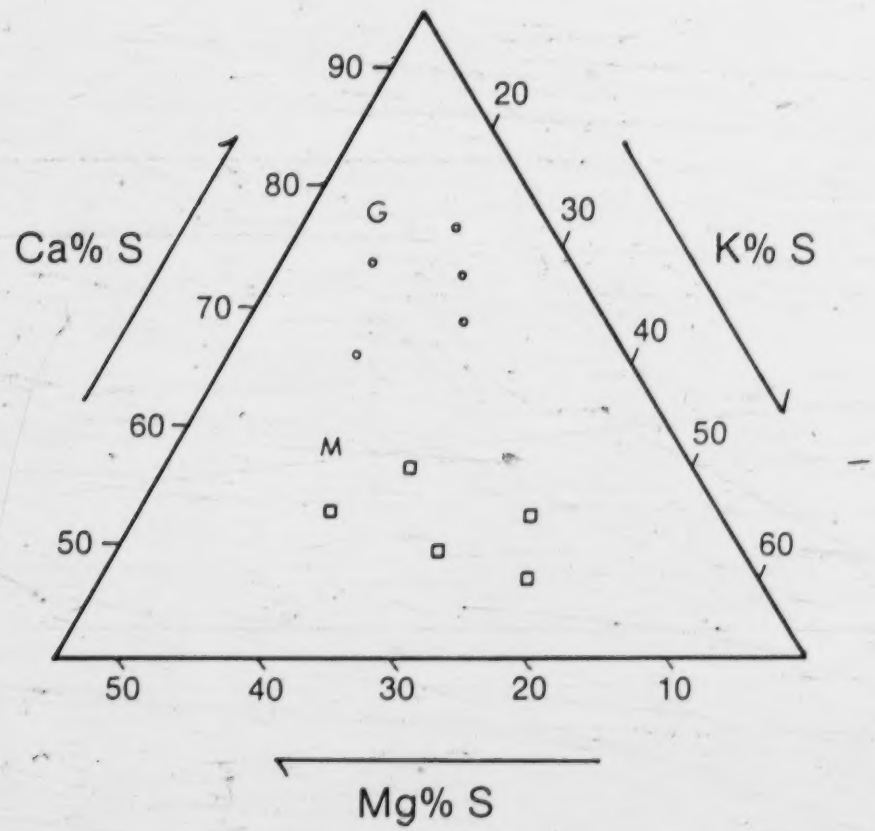
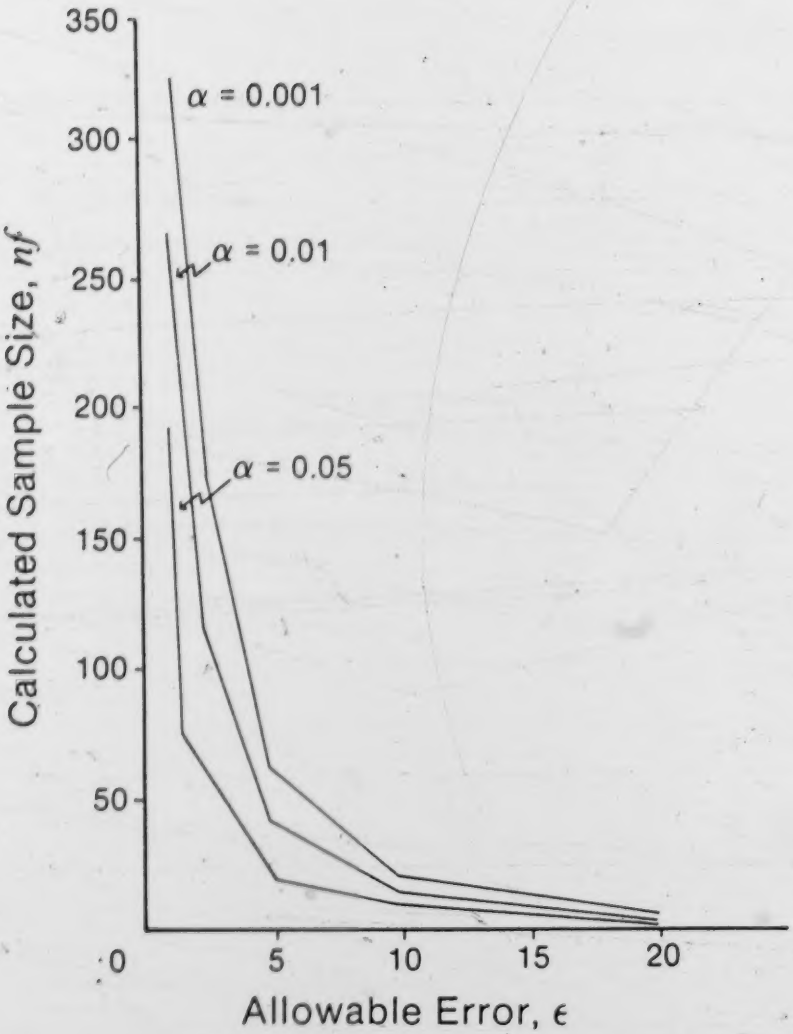


Figure II.2. Average relationship among calculated sample size (nf), allowable error(ϵ) and risk(α). Example with foliar nitrogen concentration. (from Bergland *et al* 1976).



Ca are immobile so their contents increase with age. Usually, current year's growth is analyzed, as N, P and K levels show a high correlation with soil solution nutrient concentration (van den Driessche 1974). Thus foliage analysis may be used to infer soil nutient availability and site index (van den Driessche 1974).

Because of variations in concentration over the growing season as leaf dry weight increases (van den Driessche 1974) - the rate of change being lowest in the fall and winter - sampling is often done during the dormant period, when plant nutrients may be more in equilibrium with soil nutrients and needles may be least likely to be affected by confounding physiologic changes. This keeps growth dilution and luxury comsumption separate from any interactions between genotypic and environmental effects.

Mergen and Worrall (1965) based their interpretation of seed source X environment interaction in *Pinus banksiana* seedlings on N,P, K and ash contents as a percent of needle dry weight, as did DuCros and LePoutre (1983) with *Fagus silvatica* . There were no provenance effects in *Fagus sp.*, however Ca, Mg and K levels were higher on alkaline than on acidic substrates. No detectable differences appeared with N, Fe or Zn. To use foliage analysis, it is important to relate nutrient concentration differences among provenances to yield differences, therefore results should be expressed as a percent of tissue dry weight or foliage area.

Steiner *et al* (1980) analyzed *Betula papyrifera* seedlings for Ca, Co, Al, B, and Mn content in an attempt to relate differences among provenances to differential Al tolerance. Foliar content changes could be due to reduced foliage growth in Al-injured plants since accumulations are expressed on a dry weight basis. As there were no consistent differences between tolerant and non-tolerant groups in the accumulation of any element, foliar elemental levels were only remotely involved in mechanisms of Al toxicity and they were not good indicators of Al tolerance. Van den Driessche (1974) warned of sampling seedling foliage at different developmental stages. Variations in growth attained by provenances during the test period would lead to nutrient concentration differences that may not occur in the mature foliage of older trees.

Smith *et al* (1981) tested the effects of leaf weight on interpretation of foliage analysis by sampling new and old needles seasonally in coastal and inland *Pseudotsuga menziesii* seedlings. They determined that mineral composition as a percent of dry weight is confounded by seasonal changes in carbohydrate reserves and found a better estimate in the use of elemental content per unit of leaf area. Again, there were environmental effects as the two sites imparted an effect on tree metabolism.

Field sampling results may often be masked by other influences not related to the intended main treatment effects. There may be temporal differences in foliage elemental status as a result of dry or wet years (Leaf *et al* 1970). These workers observed low values of ash %, N and K, and higher values of P as a % of ash, Ca as a % of ash and Mg concentration in *Pinus resinosa* plantations in dry years.

Bergland *et al* (1976) agreed that three sources of variation contribute to the measured variability of foliage analysis plantations:

1. temporal (year to year) variation,
2. spatial (site) variation, and
3. treatment variation.

As these factors induce heterogeneity of foliar measurements, sample size must be increased to keep specific risk and allowable error levels at certain levels over those required if variance on treatments and control plots is more homogeneous.

III. MATERIALS AND METHODS

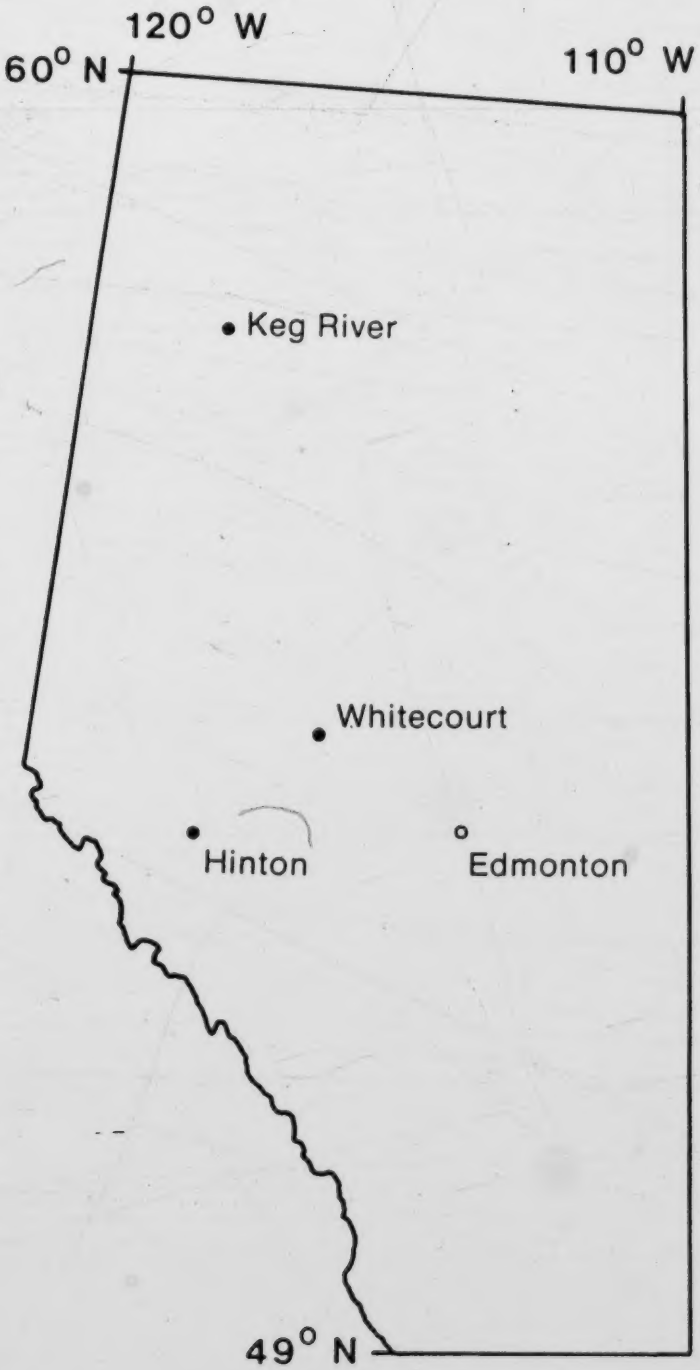
A. SITE SELECTION AND CONE SAMPLING

It has been theorized that G X E interactions are best resolved using material that has been subjected to intense natural selection (Mergen *et al* 1974, Burdon 1977). For this reason, the seed sources for provenance tests were to be from field sites that were as diverse as possible with respect to soil pH; the cone collections represented provenances from the extremes of the soil pH range for white spruce in Alberta. Using soil survey and forest cover maps, three regions of Alberta were chosen for their potential in meeting the soil selection criteria and for a natural occurrence of white spruce stands. Three stands were chosen in each of three regions so that within-region variation in soil chemical properties could be assessed and would not mask the main effects of soil chemical differences among regions. The regions are referred to by the towns they are near: Hinton, Whitecourt, Keg River (Figure III.1). Location of sites within each region are described in Appendix E.

For soil and cone sampling, there were two major criteria by which candidate sites were chosen. First, the pH in the upper solum had to be within a specific range. In the Hinton region, selected sites had a pH between 7.5 and 8.5 in the upper 0.5m of soil. Moderate to high effervescence showed these sites to be high in carbonates. Whitecourt sites were less alkaline; within the upper 0.5m the pH varied from 5.5 to 6.5 while towards lower depths, alkalinity increased to pH 7.0 or higher. Keg River sites were chosen for moderate to extreme degrees of acidity; pH readings were below 5.5 throughout the profile. As a second criterion, poorly drained sites were avoided in all regions to prevent the inclusion of trees adapted to extremes of hydrologic conditions.

As the second criterion for stand selection, each site contained at least 15 white spruce trees bearing abundant cones. The stand did not need to be pure; white spruce was often dominant or co-dominant with *Abies balsamea* or *Populus balsamifera*. Trees were selected at random within an approximate area of 1 ha, ensuring that the open-pollinated trees within sites

Figure III.1. Location of the Hinton, Whitecourt and Keg River study regions.



possessed a high degree of genetic similarity. An exception was the Keg River 'C' site, where only 14 trees were found in close proximity. Additional trees had to be sampled approximately 200 meters away from the border of the stand. Within each of the three regions, the three stands were a minimum of 0.4 km apart.

Dobbs *et al* (1976) and Winston and Hadden (1981) reported that a period of rapid embyonic development occurs immediately after fertilization in spruce, and that by early or mid-August, embryonic development will have stopped. For cone collection in 1982, between 14 and 21 trees were felled in each stand in late August and early September, before seed dispersal. Other cone collection methods, such as using pruning shears and shooting the treetops, proved to be difficult if not wholly unsuccessful in the tall, dense stands off the roadside. The first growth experiment consumed all of the seeds from some of the trees, so to replenish seed supply, 6 to 10 additional trees were felled at each site in the autumn of 1983.

Cones were transported from the field in paper bags and placed in an oven at 30° C for 12 hours to accelerate opening. The presence of insects was denoted by premature browning or bored holes and the presence of *Chrysomyxa* sp. of fungi by an orange-brown rust on the cone scales (Dobbs *et al* 1976). Infected cones were discarded to prevent contamination of seed. Seeds were shaken from the cones and sealed in plastic bags to prevent moisture loss. The seeds of each mother tree deposited in one seed bag, are hereafter referred to as a family and were stored at 5° C, a temperature that Winston and Haddon (1981) claimed would minimize dormancy and replace the need for cold stratification. Under these conditions, the viability of the seeds remained high, even after 14 months of storage. In lots of 100, the seeds of each family were germinated on moist filter paper in Petri dishes for 14 to 21 days to assess the percentage of viable seed. Coles and Fowler (1976) attested to the utility of this measure in establishing the degree in tree inbreeding. From such tests, strictly selfed seed would be expected to have a lower germination capacity, compared to natural wind-pollinated seed, where ovulate cones are fertilized by a pollen cloud to which all reproductive members of the stand contribute.

B. SOIL SAMPLING AND SITE ANALYSIS

Two soil pits were dug at each site on mid- to upper-slope positions, near as many mother trees as possible. The profile was described to a depth of 110 cm or more, according to the Canada Soil Survey Committee (1978). Samples of soil were removed from the approximate middle of each horizon or at regular 10 cm increments, placed in polyethylene bags and sealed. Soil was collected from 2 or 3 faces of the soil pit and each contributed nearly equal amounts to the composite. As Peterson and Calvin (1965) stated, such a sampling technique provides an estimate of the mean value for the horizon or profile depth. The precision with which the means were measured could not be estimated, because subsamples of the composite were not analyzed to yield an estimate of variation. For this study, where the requirement was to quantify the soil chemical component, analysis of each composite sample for each element was performed only once.

Plant community descriptions were compiled by estimating the following parameters in each stand:

1. percent cover in the moss, grass, herb, shrub and tree strata,
2. dominant species present in each stratum, and
3. regeneration status of tree species.

As an approximation of site productivity, diameter at breast height, height, and number of growth rings were recorded for 6 to 10 felled trees at each site. Numerous floral species, co-evolved into discernable communities or 'ecological species groups' (Pregitzer and Barnes 1982), indicate similar habitat conditions or they may reflect the magnitude of vegetative competition affecting tree regeneration (Eis 1981). Soil drainage, texture and fertility can be assessed from the presence of such species associations, however, only an approximate measure of habitat conditions was necessary here.

C. LABORATORY ANALYSES

Chemical analyses of the soil profile samples provided a basis for describing the comparative nutrient status of the stands. Samples were air dried immediately upon return from the field, ground to pass through a 2 mm sieve and stored at 5° C.

C.1. Exchangeable cations

Displacement of exchangeable cations was achieved by the addition of excess 1N ammonium acetate, buffered at pH 7.0 (Thomas 1982). The method is simple and quantitative except for the elements calcium and magnesium in soils having free carbonates or gypsum (Thomas 1982). Some soils from the Hinton region will have this complication. Because there is no other satisfactory method of estimating exchangeable calcium or magnesium in the presence of free carbonates, the ammonium acetate method was applied to these soils as to the others. The Mg and Ca results for the Hinton-region samples must be regarded as approximations only. The concentration of Ca^{2+}, Mg^{2+}, K^{+}, Na^{+} were determined using a Perkin-Elmer Atomic Absorption Spectrophotometer, Model no. 503. A Hamilton Digital Dilutor was used to dilute extracts with elemental concentration exceeding the standards. Concentrations of exchangeable cations are reported as mmoles of element$\cdot g^{-1}$ of oven dry soil.

C.2. PH

The pH was determined in a 2.5:1 (mL/g) water-soil suspension. The use of water has been shown to be equal in accuracy to measurements made with salt suspensions (McLean 1982). He reported that, although pH values in 0.01M $CaCl_2$ tended to be slightly lower, they were highly correlated with those in water. In a sample of 240 soils, the correlation coeffient, r, between values taken in water vs. those in 0.01M $CaCl_2$ was .939. Readings were made using a Fisher pH Meter, model no. 630, equipped with a glass electrode-calomel electrode assembly, which allows 'suspension effects' to be corrected (McLean 1982). The pH is reported to the nearest 0.1 unit.

C.3. Aluminum

Extraction techniques using unbuffered salt solutions are best suited for measuring exchangeable aluminum (Barnhisel and Bertsch 1982). The species removed by the extractant are likely monomeric and polymerie hydroxy-aluminum forms, released either from clay mineral structures or discrete noncrystalline phases. There is some uncertainty as to the involvement of these entities in actual surface exchange reactions. Nevertheless, the unbuffered salt solution provides a useful approximation of the plant-active aluminum pool. Nonexchangeable Al sources, organically-bound species, and noncrystalline stable forms of Al are not removed.

1N Potassium chloride extracts were analyzed by atomic absorption spectrophotometry, using the same equipment as for the determination of exchangable cations. Standards were made using KCl solutions of molarity equal to the soil extracts (Barnhisel and Bertsch 1982). Results are expressed as mmoles $Al \cdot g^{-1}$ oven dry soil.

C.4. Iron

Neutral 1N ammonium acetate was used to displace water-soluble and exchangeable iron for a measure of extractable Fe. It is expected that in well aerated alkaline soils, little or no exchangeable Fe will be detected as the hydrolysis of Fe to $Fe(OH)_3$ leaves the iron in a nonextractable form (Olson and Ellis 1982). Also, by dissolving some organic matter, the extractant may yield erroneously high results. A more accurate plant availability index may be obtained from the use of DTPA or HEEDA as chelating agents to stabilize extractable iron forms. However, due to the expense and scarcity of such compounds, this was not attempted.

In the assay, 1N ammonium acetate served as the extractant. The filtered extracts were evaporated to dryness at 60° C, followed by the addition of a small aliquot of concentrated HCL and HNO_3 to oxidize the organic matter. Again, the solution was evaporated to dryness and the residue was dissolved in 0.07N HCl for iron determination on the atomic absorption spectrophotometer (Olson and Ellis 1982). Ammonium acetate-extractable Fe is reported to

the nearest 0.01 mmoles of $Fe \cdot g^{-1}$ of oven dry soil.

C.5. Total carbon, carbonates and bicarbonates

Total carbon determinations involve the quantification of both inorganic and organic forms. The technique employed here was a dry combustion method which oxidizes the organic carbon to CO_2, and causes thermal decomposition of carbonate minerals or inorganic carbon (Nelson and Sommers 1982). The sample was burned in a stream of oxygen in a Leco Carbon Determinator, model no. 781-000, and the CO_2 evolved measured by a solid state infrared detector (Nelson and Sommers 1982). The total carbon results were calculated and displayed to the nearest 0.001% C on the control console, model number 780-000.

Inorganic carbon was determined by the acid neutralization method (Allison and Moodie 1965). The method provides only a rough index of carbonates as other soil constituents may react with the acid to some degree.

Soil samples were treated with suffcient hot dilute acid to decompose all carbonates. Using the method of Harris and Kratochvil (1974), the HCL stock solution was standardized by titration with a primary standard of Na_2CO_3 and then used to standardize the NaOH solution. Then the filtered soil extracts were titrated with the NaOH solution to an endpoint of 8.2 using a Radiometer Automatic Titrator model 11 equipped with a pH meter model 28. Volumes of titrant added to neutralize the remaining HCl in the extracts were recorded to the nearest 0.02 ml. Carbonates were calculated as follows:

$$CO_3\text{-}C, \% = \frac{\text{meq HCl added - meq NaOH used X 0.006 X 100}}{\text{g dry soil}}$$

C.6. Ammonium- and nitrate-nitrogen

Bremner and Keeney (1965) reported that equilibrium extraction of a soil with 2M KCl (10 mL $\cdot$ g^{-1}) of dry soil gave a quantitative recovery of NO_3^- and NH_4^+. Equilibrium extraction yields essentially similar results as thorough leaching with extracts, yet is easier,

convienient and allows a smaller volume of extract to be analysed. The extractant:soil ratio is crucial to ensure quantitative and repeatable results.

The extracts were analysed for NO_3-. and NH_4-nitrogen content using a Technicon autoanalyser II and results reported to the nearest 0.01 ppm. The autoanalyser employs a Cu-Cd reductor column to convert nitrite to nitrate, which then reacts with sulfanilamide and N-1-napthylethylenediamine to from a colored dye. The ammonium determination utilizes the Berthelot reaction, wherein a colored compound is formed by addition of Na-phenoxide and Na-hypochlorite to the solution containing ammonium.

C.7. Extractable phosphorous

The extraction of phosphates by 0.5N HCl and 1.0N NH_4F is a widely used availability index of P. Calcium, aluminum, and iron phosphates are dissolved by virtue of the complex ion formation of the metal ions in acid solutions (Olson and Sommers 1982). Although the method is most suited to acid or neutral soils, a good correlation between extractable P and plant response to added P on calcareous soils was found using soil:extractant ratios of 1:50 instead of 1:7. With excess acid added to neutralize the carbonates, the 'Bray' method was applied to calcareous soils also (Olson and Sommers 1982). The detection instrument was the autoanalyzer used in the mineral nitrogen determination.

C.8. Foliar analysis

The diversity of organic and inorganic forms of elements in plant tissue and concentration levels spanning several orders of magnitude has made tissue analysis difficult and laborious (Spiers 1982). Inductively coupled plasma-atomic emission spectrometry (ICP-AES) minimizes these complications using a high temperature argon plasma excitation source. The operation is rapid and simplistic, with up to 19 elements analysed using one digestion and no need for serial dilutions.

On the advice of Mr. S.C. Zoltai, research scientist at the Northern Forestry Centre, Canadian Forestry Service, a dry ashing technique was followed. Foliage was cremated in porcelain crucibles in a 470°C muffle furnace for 16 hr. Ashed residual material was dissolved in 1.5N HCl and HNO_3 acids, heated, dried, redissolved, filtered and made to volume. Sample extracts and internal standards were processed on an ICP-AES unit at the Northern Forestry Centre. Calcium, Mg, K, Mn, Al and Fe contents were expressed as parts per million on a 70°C-dried-tissue dry weight basis.

D. EXPERIMENTAL DESIGN AND STATISTICAL ANALYSES

An experimental unit is defined by Steel and Torrie (1980) as the entity to which one or more treatments are applied. The preplanned grouping of treatment applications on experimental units is termed the design of the experiment and is chosen according to research objectives, i.e. whether one treatment is to be monitored, two treatments compared, or several levels of two entirely different factors evaluated (Little and Hill 1978). In all designs, experimental units are classified by the treatment or treatment combinations applied and are further grouped into blocks, plots or sub-plots replicated in time or space. Each grouping will be a source of variation to be used in an analysis of variance or 'ANOVA'. ANOVA calculations use yield means from the groupings to derive mean squares. Mean squares from treatments, blocks and other sources of variation are compared and, with a specified degree of certainty or significance level, inferences are made regarding the effects of, or relationships between, treatments.

In the case of these progeny tests, the seedlings representing one mother tree were the experimental units and the chemically different bulked soils or hydroponic solutions, as rooting media, were the treatments.

For statistical validity, replications are contained within the progeny tests; seedlings of each family are randomly planted in different blocks within a treatment, ensuring that intraplot differences would not bias results. The inclusion of only one representative from each family

will not allow for the determination of within-family variability and the ranking of that family with others could be influenced by spatial differences in environmental factors within the treatment (Wright 1975). Hence, every treatment combination (one family grown under a specific treatment regime) was represented by three seedlings, and family performance means would be derived from the average of three values. Within-family variation in seedling performance was not assessed; only the main effects relating treatment and seed source influences were of interest. Mortality is also accommodated in the design by the use of three replicates, as a treatment combination would not be lost by the death of just one seedling.

Results were analysed to show portions of variance due to mother trees within sites (families), between sites of one area (seed source region), and rooting media (treatment). From this, the relative contribution of genotype and environment can be assessed for each trait recorded, as can the relationships between various genotypes and environments. The experiments enabled family performance to be charted in three 'environments'.

In another consideration for the physical layout of progeny tests, treatments are usually subdivided into several blocks, eliminating large plots with considerable spatial variability (John 1971). As differences among spatially separated blocks could cancel when treatments are compared, the spatial randomization and continued rotation of soils or solutions helped minimize the variability imposed by the large layouts. Without blocking, variability between treatments not due to the treatments may have been present (John 1971). For example, if the soil types had been planted side-by-side considerable variation between the treatments could have been attributed to microsite variation in the glasshouse.

In the soil composite progeny test conducted in a glasshouse, each soil treatment was divided into 11 'blocks' (trays of cavities), 10 with 40 seedlings and one with five. Within each tray, the cavities received seed from a completely random assortment of families, one family per cavity. At regular two-week intervals, the trays were systematically rotated within the total bench area to expose each to an average of conditions in the glasshouse chamber. In the gravel culture progeny test conducted in a growth chamber, each treatment was laid out as a water

bath with dimensions of 1.54m x 1.54m. Seedlings were systematically rotated with treatments at monthly intervals. Again, this minimized the influence of climatic gradients within the chamber, allowing treatment effects to be resolved without bias.

The soil composite and gravel culture progeny tests utilized a split-plot design. Levels of one factor (soil type or nutrient regime) were assigned to main plots arranged in either a randomized block (as for the soil composite and hydroponic progeny tests) or a latin square design (as for the gravel culture progeny test). The second factor (seed source) was randomized within each main treatment plot; this improved the precision for comparing the effects of a given treatment on a family.

The proposed experimental design for the soil composite and hydroponic progeny tests is depicted in Table III.1. Because high mortality decreased the sample size in the soil composite and gravel culture progeny tests, it was not possible to evaluate the within-family level of variation. For many treatment-family combinations, at least one of the three seedlings may have died; the possible variation between two surviving seedlings may have resulted in a statistically meaningless average. For reason of mortality, the ANOVA tables for the two experiments were amended to the form in appendix G. The SPSSx ANOVA (option 1) computer program available on the University mainframe is capable of handling missing data in ANOVA tables. This program was used for statistical analyses according to the manual by Norusis (1983). Records for each seedling were entered into a data file coded for the region, site within region and treatment.

The hydroponic progeny test employed a different design, with a smaller initial sample size (540 compared to 1215 planted in the soil composite and gravel culture progeny tests). Although mortality was negligible in this test, the same statistical package was used on the data as in the other two tests. As only 15 seedlings represented each family, within-family variation was not resolved. As with previous-mentioned tests, main effects of region and treatment and the interaction component were the levels of variation examined in the tables. The output resultant from execution of the ANOVA is in appendix G.

Table III.1. Proposed experimental design for the soil composite and gravel culture progeny tests. Proposed analysis of variance and valid errors.

ENTRY NO.	SOURCE OF VARIATION	DEGREE OF FREEDOM	TEST AGAINST ENTRY NO.
1	Region (R)	2	2
2	Site/R (S/R)	6	4
3	Family/S/R (F/S/R)	126	8
4	Treatment (T)	2	6
5	T x R	4	6
6	T x S/R	12	7
7	T x F/S/R	252	8
8	Rep/T x F/S/R	810	
Total		1214	

For all tests, the treatment, region and interaction effects are regarded as being statistically significant on the basis of the respective F values being above or below $p=0.05$.

The yield means for cereal cultivars grown in several different environments is often regressed on environmental means with resultant regression coefficients used to measure the production stability of the cultivar (Eagles *et al* 1977). The regressions and yield means are then used to select cultivars adapted to environments with differing productivities. Mergen *et al* (1977) stated that the adaptability of provenances is compared by linearly regressing their yield at each site on the site mean. Stable varieties have $r=0$. Adaptive varieties have $r=1$. A cultivar with higher than average yield and high r values would be more predictable and adapted to high-yield environments while lower-than-average cultivars with low r values would be most suited to poor environments. A regression coefficient computed by regressing mean values of genotypes from several environments on environmental means effectively describes genotypic response to environmental gradients (Rehfeldt 1979). Such characterization of the cultivars by the coefficients is most effective when a large fraction of the variation for G X E interactions is due to heterogeneity among regression coefficients. Simple correlations between provenance means in pairs of environments may by used to roughly evaluate the extent of provenance X habitat interactions and the roles of different habitats in maximizing genotypic differences (Burdon 1977). By regarding the performance in two environments as two distinct traits, the concept of genetic correlation between environments can be used in defining an environment which gives optimal screening of genotypes.

When interactions are significant in the ANOVA, population responses in relation to elevation, latitude or soil fertility can be examined. Campbell and Sorenson (1978) recommend a stepwise multiple regression for this. The presence of an interaction implies that the difference between levels of one factor (provenances) differs between levels of the other factor (soil type). With several provenances represented at each location, the site means may be considered to be estimates of site productivity.

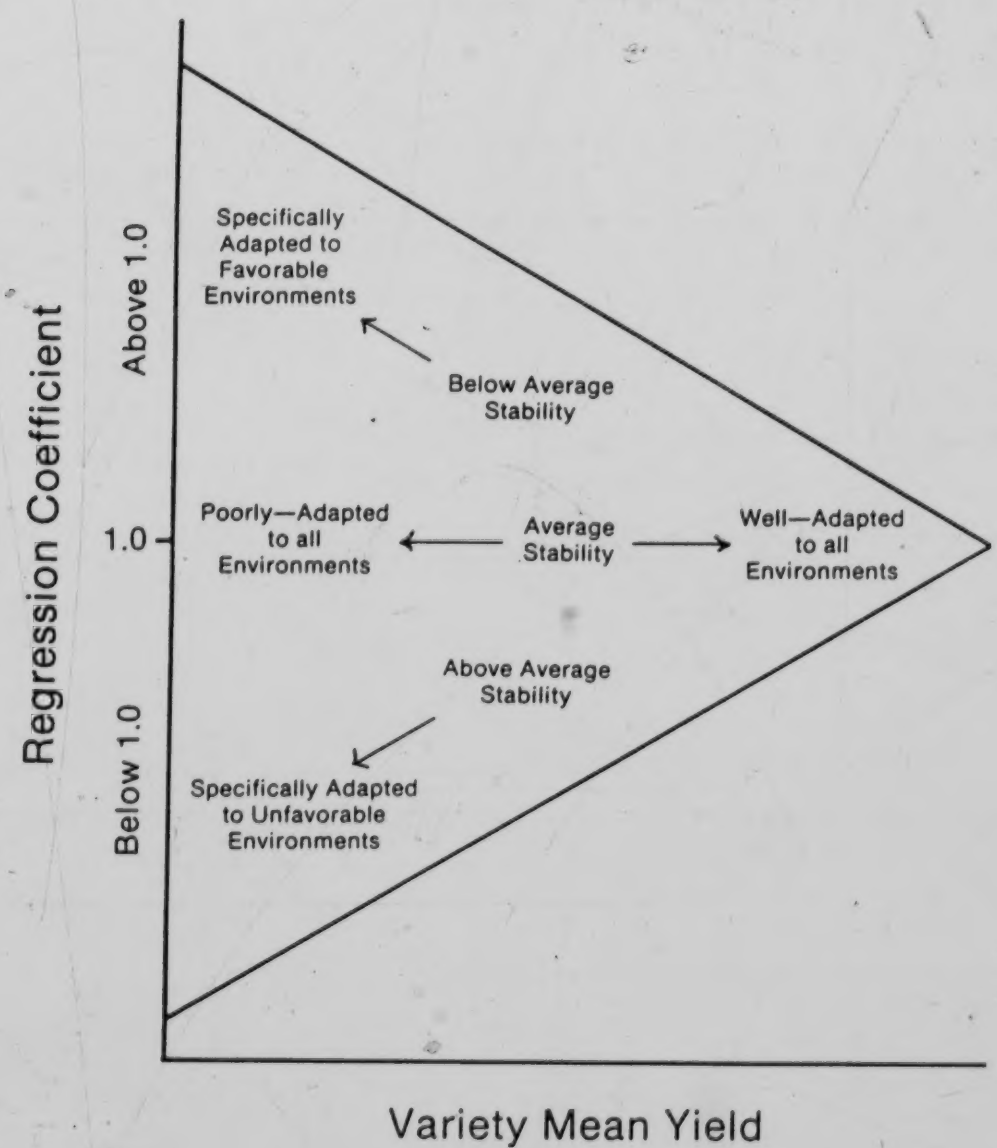
Finlay and Wilkinson (1963) suggested the measurement of yield on a log scale for a high degree of linearity. Then, the study of adaptation of all varieties could be facilitated by the use of two dimensional scatter diagrams. Mean yield and regression coefficients are the coordinates in diagrams which the authors claimed allow one to see the relationships of types of varietal adaptation (Figure III.2). Finlay and Wilkinson also expressed adaptation by plotting individual variety yield vs. site mean yield, both on a log scale. Snaydon (1962) initially proposed such log transformations of data, saying that proportional and relative differences in yield are more important than arithmetic differences.

E. PROGENY TESTS

E.1. Soil composite progeny test

For this glasshouse study, three chemically and biologically different mineral soils were composited from soil cores removed from the three sampling regions. The composited soils are referred to as 'Hinton', 'Whitecourt' and 'Keg River'. The non-sterilized soils were to represent the chemical rooting environment to which each mother tree had been subjected. To achieve this, soil cores of approximately 15 cm diameter, and 30 cm in thickness were taken from north and south orientations of each mother tree at a distance equal 3/4 of the crown radius away from the trunk. L, F, and H layers, as present, were removed so only mineral A and B horizons were included. The soil was transported in plastic bags and air-dried upon return from the field. After air drying and grinding to pass through a 2 mm sieve, each core sample was composited with others from that region and stored at 5° C. A coarse grade of inert perlite was added to the composited soil samples at a rate of 3 parts soil to 1 part perlite on a volume basis. The perlite addition was deemed necessary to enhance water holding capacity and increase aeration, thus normalizing the physical properties of the three soil composite treatments.

Figure III.2. Generalized interpretation of scatter diagrams . Variety population patterns obtained when variety regression coefficients are plotted against mean yield. (from Finlay and Wilkinson 1963).



Spencer-Lemaire 'Tinus' containers, with a total volume of 368 cm^3, were fitted with plastic mesh and perlite plugs to reduce soil slippage and filled with soil-perlite mix from one composite. The soil was leveled, compressed 3 cm, filled again and leveled resulting in a bulk density of 0.55 $g \cdot cm^{-3}$. To determine if seedlings in the containers were restricted in rooting volume, seedlings representing each of the three regions were planted in 1.5 L pots. These plants were grown in the same environment as those that were containerized and dry weights were assessed at harvest.

On each of the three soil composites, 405 seedlings were grown. Ten full trays were needed for each soil, with an additional tray holding 5 seedlings for each of the three soils. In April of 1983, seeds were germinated for 7 to 10 days in Petri dishes lined with moist filter paper. Once the radicle had emerged more than 5mm, germinants selected at random were placed in pre-moistened cavities and covered with 1 mm of fine washed sand. One family was planted at one time and the placement of the three seedlings per family on each soil type was completely random.

Daily moistening with distilled water to a predetermined approximate weight brought the soil to near field capacity without leaching. During early stages of seedling establishment, a peroidic mist of distilled water reduced desiccation and newspaper was placed above the seedlings to diffuse intense direct sunlight. The paper was removed 4 weeks after planting. Throughout the experiment, the compartment floor and wooden benches were wetted to maintain a high humidity. The day temperature was 21°C; nights were 18°C. Eighteen-hour photoperiods were maintained by using fluorescent lamps to complement natural sunlight.

At 8 weeks, mortality was assessed and empty cavities refilled with 3 to 5 seeds and covered with sand. The new germinants were later thinned to one to a cavity. During the course of seedling development, the following parameters were recorded:

1. number of cotyledons,
2. number of needles at 8, 10, 12, 14 and 16 weeks after germination,
3. stem length above cotyledons at 8, 10, 12, 14 and 16 weeks,

4. basal stem diameter at 8 and 16 weeks,

5. incidence of mortality at 8 and 16 weeks, and

6. incidence of stunting at harvest - complete cessation of needle initiation after the emergence of the cotyledons.

Brix and van den Driessche (1974) stated that nursery seedlings could occupy 700 cm^3 of rooting space three years after germination. Without fertilization, seedlings in smaller containers may be restricted by the container diameter and volume (Carlson and Endean 1976); greater volumes often translate into greater seedling dry weight, shoot length and lower shoot:root ratios. For white spruce, the researchers recommended that containers have 1:1 demensions for height and diameter, respectively. Such recommendations were not followed here because experiments conducted were of much shorter duration than nursery programs. Personal communications with Dr. A.K. Hellum of the Department of Forest Science at the University of Alberta indicated that a volume of 250 cm^3 or more would be ample rooting space for seedlings up to seven months. To confirm the assumption that the size of the Spencer-Lemaire cavities did not restrict root growth or alter seedling productivity, a random sample of seed from all 9 stands was planted in 1.5 liter pots for each of the three soil composites.

At the time of harvest, non-stunted seedlings were removed from the containers and the soil soaked and gently washed from the roots. With gentle rubbing, submersed roots were freed of mineral debris; 10-power stereomicroscopic observations revealed complete cleaning with minimal distruction of roots. The seedling was sectioned into above- and below-ground parts at the root collar. Roots were weighed fresh, dried at 60° C for 24 hours and weighed again. A unit number of needles, ranging from 50 to 100, was removed from the middle portion of the stem and weighed fresh and dry. The remaining leaves, once separated from the stems and branches, were weighed fresh and dry.

Random samples of the soil from this progeny test were retained for chemical analysis so that a comparison of fertility status before and after seedling growth could be made.

To estimate the effect of mycorrhizal associations on seedling performance, a select number of root systems were examined for the percent of fine roots with fungal infections. A selection scheme was devised with the assistance of Dr. S. Navratil, Adjunct Professor in the Department of Forest Science and Research Scientist in the Research Branch of the Alberta Forest Service, Department of Energy and Natural Resources. Families were selected for mycorrhizae examination on the basis of above-ground accumulation on a particular soil. Three families whose performance means were above average were chosen from each of the three composites. Similarily, three of the poorest families were selected so a total of eighteen families were examined. From non-stunted seedlings three 3-cm segments of primary and secondary root were removed— one each from near the root collar, the middle of the root and near the tip of a deep root. In each segment, total number of root tips and the number of infected root tips were counted using a 10-power stereomicroscope. The three segments provided an average of percent infection for seedlings in the three treatments. The purpose of assessing the incidence of infection was to determine whether or not good or poor performance was associated with the quantity of infected roots.

The presence of mycorrhizal roots was indicated by one or more of the following:

1. an absence of root hairs. Fungal hyphae are generally longer and thinner than root hairs,
2. lack of uniform taper. Fine roots always taper towards the tip, whereas mycorrhizal roots are often club-shaped and have irregular diameters, and
3. presence of a brown or black mantle, sometimes covered by a silvery powder, and often having a shiny surface.

E.2. Solution culture progeny tests

Morrison (1974) claimed that solution culture methods are useful in detecting nutritional requirements, having the advantage over field test plots of strict environmental controls. The disadvantages include differences between seedlings and adults, soil and nutrient

solution differences and the abnormal fungal associations in solution-grown plants.

Frequency of irrigation and solution replacement are two variables in hydroponics work that must be addressed. Christersson (1972) noted the value of continuous solution renewal in recommending replacement every 120 hours to keep pH variations to a minimum. Hydroponic systems lack the colloidal component of soil on which a pool of nutrients is adsorbed to buffer against depletion, therefore replacement is necessary to ensure sufficient diffusion of ions to roots in solution (Nye 1969). Nutrient levels and mole ratios used by researchers are highly variable, depending not only on what plant species was being raised, but also on the frequency of irrigation and the interval of solution replacement (Olson 1944, van den Driessche 1968, Hocking 1971, van den Driessche 1974). Generally, nutient concentration increased with lower frequency of nutrient solution application. Frequent irrigation, preferred by van den Driessche and Dangerfield (1975), minimizes any increases in solute concentration due to evaporation and transpiration of the solution remaining after free drainage. One of their tests showed more salt injury and mortality in least frequently irrigated treatments.

The objectives of the gravel culture and hydroponic experiments were to observe seedling response to chemical environments that mimic nutrient availability levels of the three regions. Analysis of the soil profile samples revealed what those levels were, although they could not be directly related to the levels in solution culture. Barber (1974) cautioned that soil nutrient levels may not reflect actual availability to roots or the ability of a soil to maintain a constant supply to roots. Some conservatism should prevail in the attempt to correlate solution culture growth directly to field plots. The soil chemical analyses will not be directly related to solution composition, although they do provide an approximation of ion ratios to use.

Gravel culture progeny test

Experiments by van den Driessche (1968) and Hocking (1971) indicated solution nutrient composition required for maximum *Picea glauca* growth with several irrigations daily. Nutrient concentrations cited were applied here except for Ca, Mg, Al, and Fe, which were to be varied. The accepted level for maximal growth was used as the intermediate level,

represented by the 'Whitecourt' treatment. In the 'Hinton' solution, Ca and Mg were increased in proportion to the magnitude of exchangeable cation differences between the Hinton and Whitecourt soil analyses while Ca and Mg levels were lessened in the 'Keg River' treatment to represent the amounts of the cations found in these soils. In a reverse trend, Fe and Al levels increased from Hinton to Whitecourt to Keg River, again reflecting the relative abundance of extractable forms. The treatments, then, included a high pH/high Ca/low Al culture to mimic the calcareous nature of Hinton soils; a low pH/low Ca/high Al system representing Keg River and; an intermediate treatment of neutral pH and moderate Ca and Al levels, reflecting the relatively neutral status of the Whitecourt soil region. Below pH 5.5, there may have been some inactivation of Al^{3+} by complexation with phosphates in solution and above pH 7, hydroxyl ions may have decreased Al activity. With the reactivity of trivalent Al ions with other solution constituents, it is acknowledged that the intended Al levels for each water bath may not have been realized during the period that seedlings were subjected to the solutions. The actual soluble Al concentrations were not assessed. Iron chelates such as Fe-EDTA or Fe-HEEDA are less likely to precipitate upon small changes in pH than Fe-citrate or $FeCl_3$ (Wallace 1956). Hence in this experiment, Fe and Mg were provided as chelates of HEEDA and Zn, Cu, Mo, and Mn as chelates of EDTA. Solution chemical composition is described in Table III.2.

The gravel culture hydroponic experiment was to be self-sustaining with the same experimental design as the soil composite experiment. A system of irrigation pumps was used to periodically flood seedlings from below in the hope of eliminating the detrimental effects seen when nutrient solutions are passed over the above ground parts. The irrigation system provided equal nutrient availability to all seedlings spatially separated within one treatment.

Advice from Rudy Kroon, Phytotron manager in the Department of Botany, led to the selection of pea-sized gravel as the root support medium. Pea gravel, with particle diameters ranging from 4 to 15 mm, was rinsed free of fine particulates and acid washed to ensure inertness. It has the advantage of fast drainage, thus minimizing the algal accumulations

Table III.2. Solution chemical regimes for the gravel culture experiment (experiment 2).
(solution composition in mmol/L or umol/L). Nutrient regimes are denoted by the soil composites they represent (Hinton, Whitecourt and Keg River).

Treatment	N	P	K	Ca	Mg	Al	Fe	Na	B	Zn,Cu,Mn	Mo	pH
	mmol/L sol.							umol/L sol.				
'H'	7.2	0.42	0.51	3.74	0.45	0.22	0.10	65	18	0.30	0.007	7.5 - 8.0
'W'	7.2	0.42	0.51	1.87	0.41	0.44	0.21	65	18	0.30	0.007	6.0 - 6.5
'K'	7.2	0.42	0.51	0.92	0.37	0.67	0.30	65	18	0.30	0.007	4.5 - 5.0

commonly seen on the surface of sand cultures. The quick drainage also provides a well-aerated rooting environment yet the wetted gravel retains sufficient water as thin films to prevent root dehydration.

Three baths were built, each being 2 meters square, 13 centimeters deep and having plywood wall supports lined with polyethylene. Nine entry points were cut into each bath, sealed with contact cement, and connected with black latex rubber tubing to a 'Little Giant model 2T' pump submersed in a nutrient solution in a 135 L drum.

Germinated seedlings were placed at random in cheesecloth, on gravel-filled 660 ml plastic containers with 4 drainage holes. Gravel was filled in between the containers, so the amount of solution required to reach within 1 cm of the surface was 125 L per treatment. The gravel, after flooding, drained within 2.5 hours. Clocks equipped with tripping timers were set for 5 x 1 hour irrigation cycles to occur daily. Each cycle was separated by a 3 to 4 hour drainage cycle; nightime drainage periods were slightly longer, as evaporation losses were lessened when the lights were off. The fluorescent lighting period was 20 hours, with a supplement of incandescent lighting beginning 1 hour after and ending 1 hour earlier. This photoperiod eliminated photoperiod-induced dormancy. Light intensity was 1600 Lux with incandescent and fluorescent lamps on. Steam vents and circulation fans kept the relative humidity to a maximum. The 'day' temperature was 21° C; night was 18° C.

To account for microclimatic variablity within the chamber, chemical treatments were rotated once monthly, concurrent with a re-randomization of all seedlings in each treatment. Due to space restrictions, each bath contained only 399 seedlings not 405. The missing seedlings were balanced with respect to seed source regions and in statistical analyses, stand means were substituted for the missing data. At the time of harvest, root, leaves, stems and branches were separated. Dry weights of each component were determined, as well as a measure of leaf weight index (weight per unit number of leaves removed from the stem at a mid-height position). Mortality was also recorded at harvest; dead individuals were not included in further measurements.

Hydroponic progeny test

A third provenance test was developed with the objective of determining seed source response to aluminum only. Two treatments were used, one with aluminum, the other without. This growth chamber experiment was executed in solution cultures with an experimental design differing from the one employed for the soil composite and gravel culute progeny tests (Appendix G).

In March of 1985, seeds of randomly selected families from each of the 9 sites were germinated. After 10 days, the germinants were transferred to sand-filled trays, where they were allowed to grow for 6 weeks with daily irrigations of Hoagland nutrient solution.

Two of the three families from each site were chosen at random for transplanting to pot cultures. Five seedlings were placed in latex foam plugs and suspended on a plastic lid such that roots were immersed in a solution-filled 4 L opaque plastic pot. As two families represented each seed source site, 18 families were included, for a total of 108 pots in the experiment. Thirty seedlings represented each family (6 pots per family). After a 4-week establishment period, half of the pots from each family received 5.6 ppm aluminum ($2 mmol \cdot L^{-1}$), with all other nutrients being the same. With such an design, 15 seedlings represented each family on each of the two treatments. Solution chemical composition is described in Table III.3.

An air inlet linked to a central supply source ensured constant aeration of the pot cultures. Solutions were replaced weekly and at the end of 30 days, the seedlings were destructively harvested and growth parameters measured as in the other experiments.

Table III.3. Solution chemical regimes for the hydroponics experiment (experiment 3). PH was adjusted initially to 4.5 with HCl. Concentrations are as mmoles or μmoles per L of solution.

ION	NON-AL TREATMENT	AL TREATMENT
N	2.00 mM (0.5 as NH_4-N) (1.5 as NO_3-N)	2.00 mM
K	0.50 mM	0.50 mM
P	0.25 mM	0.25 mM
S	0.50 mM	0.50 mM
Ca	0.50 mM	0.50 mM
Mg	0.50 mM	0.50 mM
Na	0.040 mM	0.040 mM
B	0.046 mM	0.046 mM
Fe	0.075 mM	0.075 mM
Mn	9.00 μM	9.00 μM
Zn	0.80 μM	0.80 μM
Cu	0.30 μM	0.30 μM
Mo	0.05 μM	0.05 μM
Al		2.00 mM

IV. RESULTS AND DISCUSSION

For the sake of simplicity, seed source sites are denoted by abbreviations of the region from which they are derived. Hinton-region sites are thus referred to as HA, HB and HC; those from Whitecourt and Keg River regions are designated as WA, WB, WC and KA, KB and KC respectively (See appendix figures E1, E2 and E3).

A. Seed and Cone Morphology

A.1. Cone lengths and seed weight index

Cones from the nine sites varied markedly with respect to size (Figure IV.1), as did the weight of extracted seeds (Figure IV.2). For both variables, the ranges indicate that the extent of variation among families within sites is of magnitude equal to that among sites within regions. Within-site cone length ranges (Figure IV.1) are as low as 1.0 cm (HB and HC sites), to a maximum of 3.1 cm (KB site), while there is an among-site range of 1.35 cm in site medians. The notable degree of uniqueness of the KB site results from several families possessing cone lengths averages beyond 5.0 cm- a value not exceeded in the cones of any other site.

Comparing cone lengths and seed weights, there appears to be a weak connection in family rankings. From the small cones of WB and WC sites, small seeds were extracted, yet from the large cones of KB families, the seed weight index falls within range of those from other Keg River families. Hinton sites, while having only average cone lengths, have high seed weights. Neither attribute may be used to infer relative genetic superiority, as soil fertility status and metereological events should have some degree of influence on the allocation of metabolites to reproductive parts (Mergen and Worrall 1965). Any advantage presented to embryos enclosed by larger-than-average masses of endosperm will be short-lived, dissipating soon after germination. With food reserves depleted, genetic abilities and the physical environment will become the major growth determinators.

Figure IV.1. Cone length; seed source site ranges and medians. (150 cones per mean x 10 cones per family).

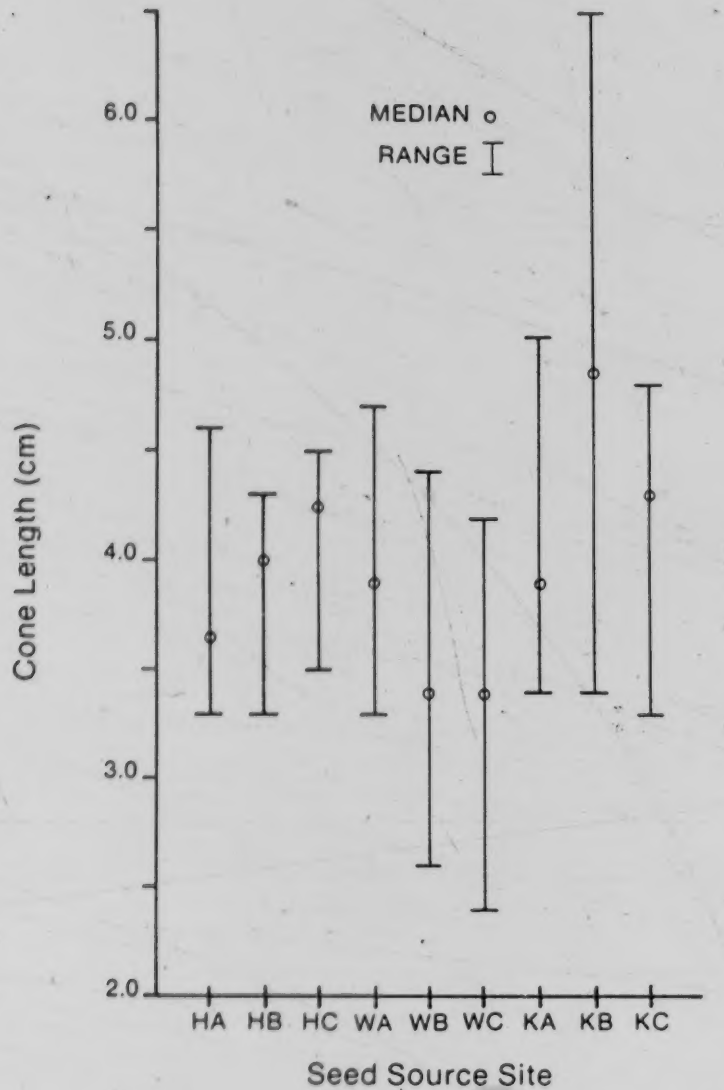
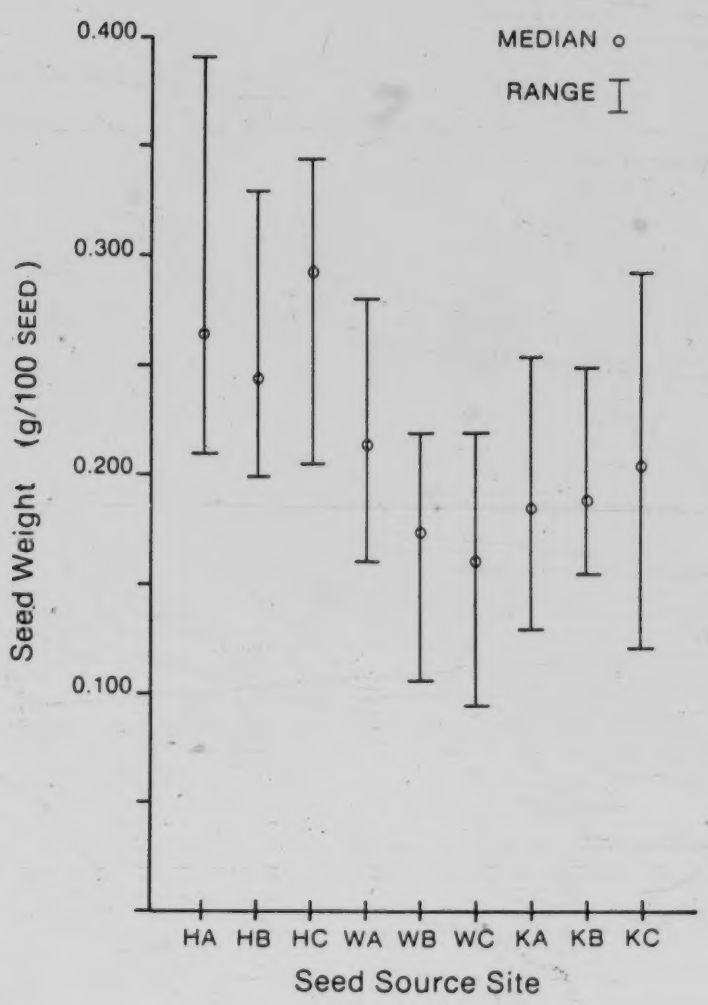


Figure IV.2. Seed weight index; seed source site ranges and medians. (10 families per mean x 100 seeds per family).



Some work has suggested that the evolutionary significance of cone length and seed weight may not be profound. In a report by Kuser and Ching (1981), highest correlation of *Tsuga heterophylla* seed weight with latitude, elevation or distance from the Pacific Ocean was $r = -0.17$, an amount not significant from 0.0 at $p = 0.05$. A correlation analysis was performed, with cone length and seed weight site medians. The results are depicted in Table IV.1.

Table IV.1. Correlation coefficients; cone and seed dimensions versus site locations.
Cone length medians and seed weight indices of families compared with elevation, longitude and latitude.

	Cone length median	Seed weight index
elevation	-.207	-.548
longitude	.601	.576
latitude	.522	-.539

The correlation coefficients are somewhat higher than those reported by Kuser and Ching (1981), possibly as an artifact of the relatively few stand locations from which the analysis was made and the close proximity of those stands. Treated singularly, each parameter is only partially responsible as determinants of cone length or seed weight. With a maximal value of $r = .60$, other site-specific variables coupled to hereditary factors would have an influence on cone length and seed weight.

A.2. Percentage of viable seed

The results of the germination test, described in Table IV.2, were not replicated for each family, hence the results should not be considered precise. Seed vitality merely approximates the relative extent of selfing in the families sampled.

With a range among the stands of 71 to 80% viable seed, it would appear that inbreeding depression is not a predominant physiologic limitation in the seed used in the progeny tests. The mother trees that were excluded from the germination test were trees that bore few cones and seeds. As the seeds germinated in this test were not planted in any growth

Table IV.2. Germination capacity of families from sampled sites.

Percentage of viable seed is determined by the use of 100 seeds for each family. Some values are missing due to shortages of seed from some families.

SEED SOURCE	TREE NO.																
SITE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Ave.
IIA	68	70	84	77	85	81	92	53	92	88		79	72	71	74		78
IIB	64	61	63	73		90	84	58	93	78	70	84	76				74
IIC	61	52	64	81	66	74	56	80	77	72	85	93	72	64			71
WA	72	76	83		81	74	59	77		76	81	83	61	82	80		76
WB	71		66		80	65	78	65	69	82	80	67	85	72	59		72
WC	66	70	71	96	84	67	90	76	92	61	82	97	77	96	74		80
KA	81	72	79	71	78	76	56	76	63	86	77	78	79	81	68	85	74
KB	67	84		73	83	68	63	88	73	96	95	92	67	74	71		78
KC	72	77	64	61	63	73	81	67	69	76	75	79	83	94			74

experiment, it would have been wasteful to allocate a large number of seeds to such a descriptive assay if they were rare.

B. Soil Composite Progeny Test

B.1. Rooting volume

The total dry weights and shoot:root ratios of seedlings planted in 368 cm^3 containers and 1.5 L pots are depicted in Table IV.3. Each reported value is derived from nine observations (three seedlings per site within region). Hence the means should be interpreted with caution; considerable performance variability at the within-region level may imply that each mean would have a very wide 95% confidence level. The results between limited and unlimited rooting volumes did not appear to differ markedly.

B.2. Performance during the test

Mortality and stunting

Following the tranplanting from Petri dishes to soil composites and after allowing a four week period for establishment, a large number of germinated plants, 327, were noted to die or suffer severe shock from the transplanting (Table IV.4). The exact cause of the phenomenon was not identified; however, it is possible that root development, while sufficient to fulfill water requirements in moist Petri dishes, was inadequate in the soil treatments. The composites were not saturated; water content was near field capacity. Hence, the soil composites may have presented plants with a stress situation. In addition, the humidity in the glasshouse compartment was much lower than in the germination environment. Water loss via transpiration may have induced an osmotic shock in the newly-transplanted seedlings. With 26.9% of the sample size lost within one month of test initiation and since germination on moist filter paper yielded seedlings with either less-than-adequate root extension or with roots unable to tolerate tranplanting, the experiment was restarted. On each cavity, 5 seeds from the

Table IV.3. Seedling shoot:root ratio and total dry weight in unlimited rooting volumes versus Spenser-Lemaire containers. 3 plants per mean. Growth period was 6.5 months.

TOTAL DRY WEIGHT (mg)

SEED SOURCE	TREATMENT (soil composite) Hinton .368 L	Hinton 1.5 L	Whitecourt .368 L	Whitecourt 1.5 L	Keg River .368 L	Keg River 1.5 L
Hinton	261	373	543	470	597	524
Whitecourt	259	240	518	438	565	573
Keg River	256	296	518	575	568	510

SHOOT:ROOT RATIOS

SEED SOURCE	TREATMENT (soil composite) Hinton .368 L	Hinton 1.5 L	Whitecourt .368 L	Whitecourt 1.5 L	Keg River .368 L	Keg River 1.5 L
Hinton	1.37	1.52	1.24	1.31	1.35	1.38
Whitecourt	1.46	1.47	1.52	1.37	1.42	1.46
Keg River	1.32	1.39	1.40	1.36	1.24	1.33

Table IV.4 Soil composite progeny test; number of dead seedlings from each seed source site prior to replanting. Hinton, Whitecourt and Keg River treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages.

SEED SOURCE SITE	Total missing	Number of dead seedlings TREATMENT		
		H	W	K
HA	20	10	5	5
HB	58	20	17	21
HC	68	26	24	18
WA	31	15	6	10
WB	24	11	6	7
WC	38	9	20	9
KA	33	15	9	9
KB	33	16	8	9
KC	22	11	3	8

b. seed source region averages.

		Number of dead seedlings TREATMENT			
		H	W	K	Ave
SEED SOURCE REGION	H	56	46	44	146
	W	35	32	26	93
	K	42	20	26	88
	Ave	133	98	96	327

appropriate family were covered with 1 mm of fine silica sand. After germination, emergent seedlings were culled, leaving one per cavity.

While mortality was substantial on all soil composites, treatment differences implied that the calcareous soil composite may be somewhat deleterious to white spruce growth; greatest losses occurred on the Hinton soil composite.

Hinton-origin seedlings suffered greater mortality than those from the Whitecourt or Keg River regions. This marked sensitivity, particularly for HB and HC seed source sites may reflect inherent anatomical development patterns in the establishment of the plant. The possibility is raised that those seed sources of highest mortality had least extensive root systems per unit of transpiring leaf surface at some period within the first 4 weeks after tranplanting. As an alternative, it is possible that the seed sources with greatest mortality were the most actively transpiring and possibly, the potentially fastest growers. The incidence of mortality and its implications will be re-examined in subsequent discussions of the results of the soil composite progeny test.

Needle number at 14 weeks

Needle number seems to support the notion that high-mortality families were also the fastest-growing (Table IV.5). Within the Hinton region, HB and HC sites had average needle numbers slightly higher than those of seedlings from the HA site. Within the other two regions, an inverse relationship between mortality and needle number did not exist and their within-region mortality values had a much narrower range. On a regional basis, Hinton seed sources had higher needle numbers than Whitecourt and Keg River seedlings, which are similar. As with the mortality data, the Hinton soil treatment was least preferential for seedling performance. Needle numbers here were nearly one-half those of the Keg River treatment.

B.3. Performance at the termination of the test

Table IV.5. Soil composite progeny test; number of needles, 14 weeks after germination . Hinton, Whitecourt and Keg River treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Average	Needle number at 14 weeks TREATMENT		
		H	W	K
HA	30	18	40	33
HB	39	23	44	50
HC	38	26	41	47
WA	32	17	37	49
WB	22	11	25	29
WC	24	12	28	33
KA	28	16	31	37
KB	28	16	33	36
KC	25	16	26	33

b. seed source region averages

		Needle number at 14 weeks TREATMENT			
		H	W	K	Ave
SEED SOURCE REGION	H	22	42	43	36
	W	14	30	35	26
	K	16	30	35	27
	Ave	17	34	38	30

Significance of F values:
Region main effect - .000
Treatment main effect - .000
Region x treatment interaction - .307

Mortality and stunting

The incidence of mortality and stunting at the conclusion of the experiment is reported in Table IV.6. The term 'stunting' refers to a state of limited seedling growth, the predominant morphological feature being the cessation of needle initiation after full expansion of the cotyledonary needles. While remaining green, the stunted seedlings are viewed as effectively dead because no stem height or needle number increments were seen during the period of free growth, when extensive biomass accumulation is expected. Mortality and stunting are jointly considered to indicate the sensitivity of root growth, in terms of maintaining physiologic functions and as an indicator of the relative severity of the nutrient regimes contained in the three soil composites.

From Table IV.6, it would appear that the Hinton seed source is collectively the most robust— able to maintain some level of growth on the treatments at a higher frequency than that achieved in the Whitecourt or Keg River seed sources. Losses of Hinton plants were nearly 50% lower than the losses of Whitecourt and Keg River regions. An analysis of frequency was not performed to ascertain the statistical significance of these differences; nonetheless H seed sources can be inferred to possess greater adaptabilty to the diversity of soil habitats presented in the test. Substantially higher losses in the other two seed source regions may reflect their lower physiologic plasticity.

While between-region mortality differences are apparent, within-region variability is also pronounced. HC and WA seed source sites are near equal, yet had mortality figures quite divergent from the other sites within those regions. By ranking mortality frequency among sites, the three H sites would be grouped in the five lowest. Whitecourt sites are extremely variable, with WB possessing greatest frequency and WA being the second lowest.

Table IV.6 indicates a very strong soil composite effect. The Hinton treatment contained more than twice the number of dead and stunted seedlings than the Whitecourt soil, which itself was twice that of the Keg River treatment. This trend indicates an increase in the suitablity of the rooting media for survival from calcareous to acidic conditions.

Table IV.6 Soil composite progeny test; number of stunted and dead seedlings. Hinton, Whitecourt and Keg River treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Total Missing	Number of stunted and dead seedlings TREATMENT		
		H	W	K
HA	43	25	9	9
HB	42	24	6	0
HC	26	15	5	6
WA	30	24	6	0
WB	59	35	17	7
WC	53	35	14	4
KA	43	30	9	4
KB	47	26	14	7
KC	58	31	17	10

b. seed source region averages

		Number of dead and stunted seedlings TREATMENT			
		H	W	K	Ave
SEED SOURCE REGION	H	64	20	15	99
	W	94	37	11	142
	K	87	40	21	148
	Ave	245	97	47	389

mycorrhizal infections

In Table IV.7, the incidence of mycorrhizal infections is described. For all but a few seed source sites-treatment combinations, over 70% of the fine roots sampled had evidence of an infection. There does not appear to be any dicsernable trends in levels of infections. For Whitecourt and Keg River seed source regions, infection levels on the Hinton soil were slightly reduced from levels on Whitecourt and Keg River soils. The Hinton seed source maintained a nearly equal level of infection on all soils. Similar infection levels were noted by Molina (1982) for *Pseudotsuga menziesii, Tsuga heterophylla* and *Picea sitchensis* mycorrhizal infections with *Laccaria laccata*.

The higher level of fungal associations of Hinton seedlings on parental soil may represent a greater potential for dry matter accumulation. However, the strength of such statements is weakened by the fact that the species involved in the symbiosis have not been identified and it is not possible to quantify the possible benefits from the infection. Holden *et al* (1983) noted that various species of fungi infecting seedlings will affect growth to differing degrees. The added influences of soil type further complicated the assessment of effectiveness of fungi in promoting seedling growth. *Laccaria amethystina* significantly improved growth in *Picea sitchensis* seedlings, compared to when *L. laccata* was used as the inoculum in nursery soils. Planting in forest soils adjusted the relative contribution of each. *Complexipes moniformis* offered no apparent benefit in either case. If genetic selectivity exists in plants with respect to fungal associations, the elaboration of fungal effectiveness for an individual tree species is further confounded.

Owing to the possibility of different fungal species being involved in the three soil composites, some uncertainty accompanies the evaluation of roles of mycorrhizae in this test. The relatively high extents of infection merely allows for the inference that, to some extent, root and whole plant metabolic processes may by mediated by fungal associations.

Table IV.7 Soil composite progeny test; frequency of mycorrhizal infections. Total number of fine roots examined and % of fine root infections.

a. seed source site averages

SEED SOURCE SITE	TREATMENT (soil composite)					
	Hinton		Whitecourt		Keg River	
	% infected	Total fine roots	% infected	Total fine roots	% infected	Total fine roots
HA	86	251	88	222	76	188
HB	84	199	78	185	78	232
HC	65	245	73	150	71	191
WA	75	213	79	153	77	190
WB	68	162	75	203	75	172
WC	67	181	85	185	82	191
KA	66	199	62	151	76	170
KB	74	216	82	212	81	163
KC	78	167	74	226	79	159

b. seed source region averages

SEED SOURCE REGION	% Fine roots infected TREATMENT			
	H	W	K	Ave
H	78	80	75	78
W	70	80	78	76
K	73	73	78	75
Ave	74	80	77	77

dry matter accumulation

Dry weight determinations from the soil composite progeny test are depicted in Tables IV.8 to IV.12. For all plant components, a strong treatment effect is evident at the $p=0.05$ level. For all seed source regions, maximal growth occured on the Keg River soil composite; least biomass accumulation was on the Hinton soil composite. The trend of increased biomass accumulation from the most calcareous (Hinton) treatment to the most acidic(Keg River) may represent the effects of both soil chemical and biological features, as they vary among the treatments.

It appears that white spruce seedlings are better adapted to more acidic conditions. By the fact that the calcareous Hinton soil held the poorest productivity potential, any harmful effects of carbonates, low H^+ concentration and other extremes of this soil solution did not seem to be ameliorated in the presence of mycorrhizae. However, to state unequivocally that the presence of symbiotic associations were not beneficial to the plants in calcareous habitats, comparisons with non-mycorrhizal seedlings in the same chemical regimes would have to be made. Dry weight averages were greatest in the Keg River soil, where amounts of soluble Al, Fe and other metallic cations may approach toxic values. Here, the potentially harmful effects of the soil solution may be buffered by the presence of mycorrhizae. Mycorrhizal roots have an identifiable need for a specific rhizosphere pH for the uptake of such anions as PO_4^{-3} in exchange for organic acids (Buwalda *et al* 1983). It is possible for a high-pH environment to disrupt this exchange.

Evaluating the positive benefits of rhizobial infections in acid and neutral soils, Rai *et al* (1982) observed greater nodule dry weights and total plant N in acid soils. At pH values higher than 6.0, the symbiotic interplay of plants and microbes became less effective. Poor seedling growth, as exhibited in the calcareous treatment of the test, may be attributed to a similar mal-adaptation of the spruce-mycorrhizal complex to soil alkalinity. The dominance of calcium over other essential cations in the soil solution of the Hinton treatment may have swamped the absorptive sites on seedling roots. An inability of the fungal symbiont to

Table IV.8 Soil composite progeny test; seedling total dry weight. Hinton, Whitecourt and Keg River treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Average	Seedling total dry weight (mg) TREATMENT H	W	K
HA	535	296	577	627
HB	513	316	516	602
HC	488	324	539	562
WA	548	271	578	651
WB	463	231	476	515
WC	472	270	480	515
KA	487	231	517	554
KB	468	257	514	536
KC	526	293	525	619

b. seed source region averages

		Seedling total dry weight (mg) TREATMENT H	W	K	Ave
SEED SOURCE REGION	H	314	543	597	511
	W	261	518	565	500
	K	259	518	568	492
	Ave	284	527	576	501

Significance of F values:
Region main effect - .093
Treatment main effect - .000
Region x treatment interaction - .970

Table IV.9 Soil composite progeny test; above-ground seedling dry weight. Hinton, Whitecourt and Keg River treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Average	Seedling above-ground dry weight (mg) TREATMENT H	W	K
HA	292	168	311	343
HB	285	185	278	337
HC	275	188	302	313
WA	300	155	313	372
WB	254	128	264	280
WC	266	155	271	289
KA	256	119	276	288
KB	257	155	280	289
KC	284	162	293	325

b. seed source region averages

		Seedling above-ground dry weight (mg) TREATMENT H	W	K	Ave
SEED SOURCE REGION	H	181	297	331	283
	W	148	286	316	279
	K	146	282	300	265
	Ave	162	289	316	276

Significance of F values:
Region main effect - .028
Treatment main effect - .000
Region x treatment interaction - .864

Table IV.10 Soil composite progeny test; leaf dry weight. Hinton, Whitecourt and Keg River treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Site average	Leaf dry weight (mg) TREATMENT		
		H	W	K
HA	188	110	203	217
HB	185	122	179	220
HC	185	125	208	209
WA	190	100	203	220
WB	160	82	163	178
WC	166	98	168	181
KA	162	77	178	179
KB	163	106	172	184
KC	182	108	189	206

b. seed source region averages

		Leaf dry weight (mg) TREATMENT			
		H	W	K	Ave
SEED SOURCE REGION	H	120	197	216	186
	W	95	181	198	174
	K	97	179	189	168
	Ave	107	186	200	177

Significance of F values:
Region main effect - .001
Treatment main effect - .000
Region x treatment interaction - .967

Table IV.11 Soil composite progeny test; leaf weight index. Hinton, Whitecourt and Keg River treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Average	Leaf weight index (mg/100 needles) TREATMENT		
		H	W	K
HA	96	85	100	97
HB	92	83	94	96
HC	93	84	98	94
WA	87	73	92	89
WB	83	65	84	87
WC	80	74	82	80
KA	84	75	86	86
KB	84	71	85	90
KC	91	78	93	94

b. seed source region averages

		Leaf weight index (mg/100 needles) TREATMENT			
		H	W	K	Ave
SEED SOURCE REGION	H	84	97	96	93
	W	71	87	85	84
	K	74	88	90	86
	Ave	78	91	90	88

Significance of F values:
Region main effect - .000
Treatment main effect - .007
Region x treatment interaction - .842

selectively exclude Ca in favor of other cations, coupled to the photosynthetic drain by the fungi, may have contributed to the impairment of seedling growth on this soil.

Vesicular-arbuscular mycorrhizal roots have photosynthetic absorption kinetics differing from those of the plant roots (Gianinazzi-Pearson and Gianinazzi 1983). Hyphae networks can efficiently explore deficient soils for relatively immobile nutrients such as phosphorous, although any enhanced efficiency of uptake is not due to a capacity to immobilize P sources unavailable to non-mycorrhizal roots. Mycorrhizae absorbed P from labile pools that were unavailable to plant roots because of hyphal lengths overcoming the limitation of diffusion and mass flow. After passing from external hyphae to internal mycelia, the absorbed nutrients may then be transported to root tissues for redistribution.

A problem arises from the determination of P availability by Ca activity. In calcareous soils such as the Hinton composite, the labile P and readily exchangeable P pools may be reduced by precipitation of basic Ca-phosphates (Mortvedt 1976).

In addition to the treatment effect, total and above-ground dry weight was dependent upon seed origin. For total dry weight (Table IV.8), the seed source region effect was not significant at $p=0.05$ while for above-ground and leaf dry weights (Tables IV.9 and IV.10), this genotype effect was significant at $p=0.05$. Comparing the total dry weight and leaf dry weight data, the difference in F value significance may indicate that the seed source effect may reside in the leaf component. Although the trend is only slight, seedlings from the most acidic region accumulate the least above-ground biomass.

These results are in agreement with those of Snaydon and Bradshaw (1962), who noted that acidic populations generally yield less than calcareous populations, even at low Ca levels in non-competitive conditions. The response differences, they said, are mediated by:

1. root morphology,
2. exchange absorption,
3. nutrient absorption rates,
4. nutrient tranlocation rates, and

5. metabolic utilization.

Recalling previously-mentioned differences in root CEC, where acid populations had higher values, and that Ca and Mg uptake may be competitive processes, then the relatively lower growth of the califuge (acid-origin) and calcicole (calcareous-origin) provenances may be accounted for.

There were no significant genotype X environment interactions in the case of total, above-ground and leaf dry weights. Hinton seed sources exhibited the best performance on the parental soil as well as the most foreign soil in terms of pH and dominant cations (Keg River soil). Keg River seedlings, which grew most poorly on the calcareous substrate, continued to be outperformed on their parental soil. Such patterns are not characteristic of those expected when an interaction effect is present.

The leaf dry weight data of Table IV.10 reveal the consistent dominance of the Hinton seed source region in ranking on all soils. Hinton seedlings collectively maintained a greater emphasis on leaf production, possibly as an ingrained strategy towards dry matter partitioning. Differences in carbon allocation patterns will be examined in a latter discussion. Table IV.11, containing the leaf weight index data, reaffirms this emphasis on leaf production in the Hinton seedlings.

Leaf weight index is derived as a relative descriptor, which may incorporate differences in leaf length, diameter and density into one measure. At the level of seed source region, the parameter may be strongly controlled genetically, as supported by the F value being significant at $p=0.05$. The Hinton seed source sites ranked as the top three for this trait, while the lowest two were from the Whitecourt region (WB and WC). The dominance of the Hinton seedlings in the averages for each soil composite would suggest an inherent emphasis on leaf production in Hinton seedlings that is somewhat greater than for Whitecourt and Keg River plants.

The index was treatment-dependent, showing increases from Hinton to the Whitecourt treatment. Apparently, as the less-than-optimal conditions of the calcareous treatment had an inhibitory effect on the roots, lesser quantities of nutrients translocated from the roots may

have caused the index on these soils to be low. Comparing the Whitecourt and Keg River soils, only the Keg River seed source region exhibited a further increase in leaf weight index. Conceivably, the earlier-mentioned positive response of the roots of Keg River seedlings to parental soil properties would provide increased substrates for leaf development. Since Hinton and Whitecourt seed sources showed no such increases, they may be regarded as lacking in the same level of adaptation of Keg River seed sources.

The seed source effect on root dry weight data (Table IV.12) was small. Although the interaction effect was not significant at $p=0.05$, performance differences between the Hinton and Keg River population in response to the treatments were evident. On the Hinton soil, Hinton seedlings combined to average 19 more milligrams of root biomass than the Keg River seedlings. However, on Keg River soil, the superiority of Hinton provenances is lost and the ranking is reversed. Keg River seed sources collectively average 2.5 mg more than the H seed sources on the parental Keg River soil. While this trend was not significant, likely due to wide confidence intervals around the means, it does raise the possibility of specific adaptability of roots of K seedlings to conditions imposed by the acidic habitat. On the other hand, Hinton seed sources are more broadly adaptable, capable of relatively good growth on acidic soils, yet not incurring the same degree of growth inhibition on the Hinton soil.

Although at the regional level, an interaction was evident in root dry weight data, the large within-region variability detracts from its statistical significance. Similar to total dry weight data, HA, WA and KC attained the highest ranks. Seedlings from the HA site were above-average performers on all soils. Sites HB and HC, while above average on parental soil, were frequently below average on others, indicating specific adaptability to soil conditions. HB, HC and KA were intermediary; WB, WC and KB constituted the poorest performers overall in both above- and below-ground plant compartments. However on the least productive Hinton soil, the ranking of WA declined and all three Whitecourt sites were then below average. Appendix Figures H1 to H5 contain a graphic presentation of the within-region responses from the soil composite progeny test.

Table IV.12 Soil composite progeny test; root dry weight. Hinton, Whitecourt and Keg River treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Site average	Root dry weight (mg) TREATMENT		
		H	W	K
HA	243	128	266	284
HB	228	131	237	266
HC	213	137	237	248
WA	242	117	266	275
WB	209	102	212	235
WC	206	115	209	226
KA	231	112	241	266
KB	211	103	234	247
KC	242	130	232	294

b. seed source region averages

		Root dry weight (mg) TREATMENT			
		H	W	K	Ave
SEED SOURCE REGION	H	133	246	265	227
	W	113	232	248	221
	K	114	236	268	227
	Ave	122	239	260	225

Significance of F values:
Region main effect - .167
Treatment main effect - .000
Region x treatment interaction - .881

Above- and below-ground dry weight data, combined into a ratio is reported in Table IV.13 to illustrate differences in partitioning of biomass into these two components on different treatments. The soil composite effect was negligible as the significance of the F value was .462, while the seed source effect was of greater importance with the significance of the F value being .067. Among the most notable features were the highest ratio being found with Hinton seedlings on Hinton soil, while Keg River sources on Keg River soil constituted the lowest ratio.

The observed relationship disagrees with one observed by Keyes and Grier (1981) in 40-year-old *Pseudotsuga menziesii* stands on low and high productivity sites. A greater investment of fine roots was apparent on the harshest sites of their study. as these seedlings required a greater energy expenditure in terms of fine root growth. The harshest treatment of the soil composite progeny test was the Hinton soil and here, root accumulation was the lowest of all treatments. Mycorrhizae of *Pinus taeda* seedlings were found to lose up to 3.5 times more carbon by root respiration in comparison to non-mycorrhizal plants (Reid *et al* 1983). It is possible that the advantageous fungal-root complex in the non-calcareous soils may have converted a greater proportion of diverted reduced carbon to energy maintainance for metabolism and biomass. In the calcareous condition, non-beneficial symbiotic infections may have generated a sufficient sink demand for carbon, thus yielding a shoot:root ratio higher than that of other treatments.

If an adaptive strategy is ingrained in such seed sources, it would appear that the Hinton seed allocates a slightly higher proportion of photosynthate to above-ground biomass, while for Keg River plants, a greater emphasis is placed on root development. In the high-pH condition of the Hinton soil, the rooting development of the Hinton and Keg River provenances is was somewhat less than in the acidic condition (Table IV.12). Ratios were comparatively lower on the Keg River soil (Table IV.13). The Keg River habitat may be more conducive to root establishment by virtue of the advantageous fungal association present or its fertility status. To a minor degree, roots of Keg River seedlings responded most favorably to this

Table IV.13 Soil composite progeny test; ratio of above- to below-ground dry weight. Hinton, Whitecourt and Keg River treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Average	Above-/below-ground dry weight TREATMENT		
		H	W	K
HA	1.26	1.38	1.20	1.26
HB	1.34	1.59	1.23	1.43
HC	1.39	1.40	1.45	1.33
WA	1.37	1.33	1.29	1.46
WB	1.38	1.31	1.37	1.41
WC	1.48	1.56	1.51	1.44
KA	1.24	1.06	1.29	1.27
KB	1.34	1.64	1.24	1.27
KC	1.27	1.24	1.40	1.18

b. seed source region averages

		Above-/below-ground dry weight TREATMENT			
		H	W	K	Ave
SEED SOURCE REGION	H	1.45	1.30	1.35	1.35
	W	1.38	1.38	1.44	1.41
	K	1.34	1.31	1.24	1.28
	Ave	1.40	1.33	1.35	1.36

Significance of F values:
Region main effect - .067
Treatment main effect - .462
Region x treatment interaction - .616

medium; root weights per unit amount of dry matter accumulated were highest for this seed source. In being capable of accumulating more biomass for above-ground parts, Hinton seedlings display greater adaptability to the Hinton soil. On average, Hinton seedlings may have evolved a higher level of resistance to soil alkalinity or they may be more efficient in selectively absorbing some nutrient from the soil with free carbonates present.

seedling dimensions

With regards to volume measurements, stem height and root collar diameter are given in Tables IV.14 and IV.15 and are graphed in Appendix Figures H10, H11 and H12. The trends lying within each treatment are difficult to discern because of the large variation among sites within each region. Hinton sites have the greatest diameters on the Hinton soil composite. The WA site was clearly outstanding on all treatments. The apparent poorer ranking of the WB and WC seedlings would seem to eliminate any possible existence of a distinct positive adaptation of the Whitecourt seed source region as a whole to the Whitecourt soil type. Similarly in the Keg River treatment (Appendix Figure H12), the reasonably good position of KA and KC sites is not a character shared by the KB site. Again, while some degree of adaptability is shown by the volume response of some sites to some treatments, the inability of the adaptability to persist in all sites of that region raises a question to the existence of G X E interactions.

In an already mentioned trend, volume appears to increase along the Hinton to Whitecourt to Keg River gradient. For root collar diameters, the Hinton seed sources measured slightly larger. Seed source did not significantly affect stem height. The treatment effect was very strong, supporting the typical effect of site on height growth.

Table IV.14 Soil composite progeny test; stem height above cotyledons. Hinton, Whitecourt and Keg River treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Average	Seedling stem height (mm) TREATMENT H	W	K
HA	81	55	85	91
HB	79	57	82	87
HC	80	61	90	84
WA	93	61	96	105
WB	79	53	83	82
WC	83	50	85	89
KA	84	47	92	90
KB	77	60	82	82
KC	85	58	90	92

b. seed source region averages

		Seedling stem height (mm) TREATMENT H	W	K	Ave
SEED SOURCE REGION	H	59	85	87	80
	W	56	89	93	86
	K	56	88	88	82
	Ave	57	87	89	82

Significance of F values:
Region main effect - .446
Treatment main effect - .000
Region x treatment interaction - .846

Table IV.15 Soil composite progeny test; root collar diameter. Hinton, Whitecourt and Keg River treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Site average	Root collar diameter (mm) TREATMENT H	W	K
HA	1.8	1.6	1.8	2.0
HB	1.8	1.6	1.8	2.0
HC	1.8	1.6	1.7	1.9
WA	1.8	1.5	1.8	2.0
WB	1.7	1.3	1.8	1.8
WC	1.7	1.5	1.7	1.8
KA	1.7	1.4	1.7	1.9
KB	1.7	1.4	1.9	1.7
KC	1.8	1.5	1.8	2.0

b. seed source region averages

		Root collar diameter (mm) TREATMENT H	W	K	Ave
SEED SOURCE REGION	H	1.6	1.8	1.7	1.8
	W	1.4	1.8	1.9	1.8
	K	1.4	1.8	1.8	1.7
	Ave	1.5	1.8	1.9	1.8

Significance of F values:
Region main effect - .026
Treatment main effect - .000
Region x treatment interaction - .133

C. Gravel Culture Progeny Test

The second experiment to be discussed features plant response to nutrient solutions in a gravel support matrix. The physical design, previously untested in the University Phytotron facilities, failed to sustain a level of growth as vigorous as that seen in the soil composite progeny test. In an estimation of seedling health, a grading system was established to account for stunting, chlorosis and necrosis. Assessments were scaled from 1 to 5, with 1 being the seedlings of poorest vigor. Classes were dominated by the following morphological qualities:

1. severely stunted and/or completely necrotic or nearly so,
2. very stunted and/or very necrotic,
3. slightly stunted and very chlorotic,
4. not stunted but very chlorotic, and
5. not stunted and not chlorotic.

The seedlings of vigor ratings in classes 1 and 2 were deemed to be responsive to environmental factors that were not part of the treatments. With negligible growth increments, the effect of the applied treatments could not be evaluated, hence these seedlings were not included in the analysis of variance. The number of seedlings falling into categories 1 and 2 is reported in Table IV.16. As the evaluation of vigor was visually-based, it was not possible to distinguish dead seedlings from those that were only severely stunted and not yet dead; mortality and stunting are listed together with no attempt made to separate them.

Greatest stunting and mortality occurred on the acidic 'Keg River' gravel culture, decreasing to be least on the 'Hinton' gravel culture (Table IV.16). Noting that mycorrhizal influences were to be minimized in this test, freshly prepared nutrient solutions, acid-washed gravel and perchloric acid-washed seed were used. While the nutrient solutions were not necessarily organism-free, normal mycorrhizal associations with roots were not present. Their absence may be used to explain why the low pH-high Al treatment was least conducive to seedling establishment. The Hinton and Keg River seed sources had relatively low fatality rates, compared to the Whitecourt seed sources. Keg River seed appears to be slightly more

Table IV.16 Gravel culture progeny test; number of stunted and dead seedlings. 'Calcareous', 'near-neutral' and 'acidic' treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Total missing	Number of stunted and dead seedlings TREATMENT		
		H	W	K
HA	32	1•	17	14•
HB	65	20	24•	21
HC	32	11•	8	13•
WA	51	12	20•	19•
WB	64	21	19•	24•
WC	49	12•	19	18
KA	32	0	9•	23•
KB	42	8•	11•	23
KC	39	1•	14	24•

b. seed source region averages

		Number of stunted and dead seedlings TREATMENT			
		H	W	K	Ave
SEED SOURCE REGION	H	32	49	48	129
	W	45	58	61	164
	K	9	34	70	131
	Ave	86	141	179	406

•denotes treatment combinations where 44 seedlings were planted, not 45.

adapted to the Hinton treatment, just as Hinton seed is on the Keg River gravel culture.

Among possible flaws of the design was the use of pea gravel with high light reflectance. Leaf temperatures may have exceeded normal values, as the gravel surface reflected light from the overhead lamps. To prevent overheating in the growth chamber, the use of heat-emitting incandescent lamps was kept to a minimum. From this, a second inhibitory factor may have arisen. The fluorescent lamps emit light in proportions skewed to the blue end of the spectrum. Deficiencies of red and far-red light may have contributed to the lack of stem elongation, a predominant character in most seedlings from this test.

As a final technical difficulty, the periodic irrigation of seedlings in gravel was occasionally interrupted by time clock failures, power failures and plugged pumps. Despite daily monitoring for such events, it is possible that 1 or 2 of the 5 daily watering cycles may have been eliminated when problems occurred. The rapidly drained gravel may then have desiccated, especially in the upper few centimeters, to the point of harming the plants. The need to supply adequate amounts of mineral nutrients in a small volume of nutrient solution has led to the use of initially high ion concentrations in many soil-free growth experiments (Asher and Edwards 1983). This may have subjected seedlings to deleterious conditions, at least temporarily. This feature of culture experiments, coupled to the possibility of large changes in nutrient concentrations occurring over the two-week depletion period for solutions in this test, may point to the essentially unbuffered solutions as the origin of the tests limitations.

dry weight accumulation

The three gravel culture treatments differed significantly in their productivity potential, as presented by seedling total dry weight averages and accumulated biomass in individual plant compartments. Tables IV.17 to IV.19 reveal that total and above-ground dry weight means were slightly higher for the Whitecourt treatment, compared to those of Hinton and Keg River. The acidic treatment induced the lowest biomass increments, overall. Containing the least extreme levels of Al, Ca and pH, the Whitecourt gravel culture may represent the least adverse

Table IV.17 Gravel culture progeny test; seedling total dry weight. 'Calcareous', 'near-neutral' and 'acidic' treatments are referred to as 'H', 'W' and 'K', respectively..

a. seed source site averages

SEED SOURCE SITE	Site Average	Seedling total dry weight (mg) TREATMENT		
		H	W	K
HA	126	106	161	122
HB	140	141	131	146
HC	135	133	150	119
WA	133	130	142	127
WB	96	85	109	93
WC	119	117	144	97
KA	146	158	131	151
KB	121	109	161	81
KC	120	127	115	111

b. seed source region averages

		Seedling total dry weight (mg) TREATMENT			
		H	W	K	Ave
SEED SOURCE REGION	H	124	149	128	133
	W	113	132	106	117
	K	133	136	114	130
	Ave	124	139	117	127

Significance of F values:
Region main effect - .149
Treatment main effect - .031
Region x treatment interaction - .723

Table IV.18 Gravel culture progeny test; above-ground dry weight. 'Calcareous', 'near-neutral' and 'acidic' treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Site Average	Seedling above-ground dry weight (mg) TREATMENT		
		H	W	K
HA	95	79	125	89
HB	108	110	99	113
HC	105	106	118	89
WA	100	97	109	96
WB	71	63	82	67
WC	89	87	111	72
KA	107	111	97	114
KB	90	80	126	54
KC	88	94	86	81

b. seed source region averages

		Seedling above-ground dry weight (mg) TREATMENT			
		H	W	K	Ave
SEED SOURCE REGION	H	95	116	96	102
	W	84	101	79	88
	K	96	103	83	96
	Ave	92	106	87	95

Significance of F values:
Region main effect - .113
Treatment main effect - .012
Region x treatment main effect - .889

Table IV.19 Gravel culture progeny test; leaf dry weight. 'Calcareous', 'near-neutral' and 'acidic' treatments ar referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Site Average	Seedling leaf dry weight (mg) TREATMENT		
		H	W	K
HA	81	64	111	76
HB	92	93	83	97
HC	89	89	101	74
WA	85	80	95	82
WB	59	50	70	57
WC	76	73	97	60
KA	90	93	83	94
KB	76	65	111	44
KC	75	78	76	67

b. seed source region averages

		Seedling leaf dry weight (mg) TREATMENT			
		H	W	K	Ave
SEED SOURCE REGION	H	79	100	81	87
	W	69	87	67	74
	K	80	90	68	81
	Ave	77	93	73	81

Significance of F values:
Region main effect - .124
Treatment main effect - .003
Region x treatment interaction - .898

rooting environment. The treatment effect was significant as $p=0.05$ for the three parameters. The seedling response pattern reflects greater sensitivity of white spruce seedlings to a high Al concentration, than to high Ca concentrations, at least in the absence of root-associated fungi.

The seed source effect was insignificant, indicating a marked lack of genetic effects in total biomass accumulation, still the overall superiority of the Hinton seed sources may be implied by the slight differences in total dry weight means. Although the trend is not statistically verified, the Hinton-origin seedlings seemingly outperformed their counterparts on neutral and acidic treatments, yet lacked this advantage on the parental calcareous treatment, where Keg River seedlings were marginally superior. Genotype X environment interactions were non-existent; any expressed trends in regional response may be artifacts induced by the high within-region variability.

Site differences within regions were also evident. Similar to several rankings from the soil composite progeny test, WB and WC site performed with consistent relative mediocrity. Other seed source sites varied in ranking between the two tests, but the seed stock from these two sites clearly revealed genetic inferiority.

Contrary to the total dry weight data, the root dry weight data (Table IV.20) possessed an insignificant treatment effect, while the seed source effect was strong (significant at $p=0.10$, but not at $p=0.05$). The average for the Whitecourt seed source region was lowest, again due to the poor showing of WB and WC seed on all treatments.

A unique trend was displayed by the Keg River population, as it yielded greatest root growth on the Hinton treatment, whereas for the Whitecourt and Keg River seed regions, maximal production was on the Whitecourt gravel culture. As an apparent anomaly, it appears that, collectively, the Keg River seedlings find the calcareous environments slightly more suitable for growth than their counterparts. It was primarily the KA site that contributed this property to the average of the region. Comparing the root and total dry weight data of the soil composite and gravel culture progeny tests, the notion is raised that adaptability to parental soil conditions, which seedlings would be expected to possess, is dependent on the presence of

Table IV.20 Gravel culture progeny test; root dry weight. 'Calcareous', 'near-neutral' and 'acidic' treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Site Average	Seedling root dry weight (mg) TREATMENT		
		H	W	K
HA	31	27	36	32
HB	32	31	32	33
HC	30	28	32	30
WA	32	33	33	31
WB	25	22	27	26
WC	30	30	34	25
KA	40	46	33	37
KB	31	29	35	27
KC	31	33	29	30

b. seed source region averages

		Seedling root dry weight (mg) TREATMENT			
		H	W	K	Ave
SEED SOURCE REGION	H	28	33	32	31
	W	29	31	27	29
	K	37	32	31	34
	Ave	32	32	30	32

Significance of F values:
Region main effect - .094
Treatment main effect - .668
Region x treatment interaction - .305

biological influences naturally present thoughout the soil and especially in the rhizosphere.

The ratio of above- to below-ground dry weight was significant for treatment and seed source effects at $p=0.05$ (Table IV.21). The low ratio in acidic treatments implies that, on a root weight basis, above-ground biomass was difficult to accumulate on that medium. High ratios on the Whitecourt treatment reflect the relative suitablity of that medium for support of leaf and stem growth. Recalling the insignificance of the treatment effect on root dry weight, the treatment effect on the ratios may be mediated through an effect on above-ground dry weight.

The three Hinton seed source sites were ranked as the highest three ratios, and the three from Whitecourt were among the four lowest. Evidently, the partitioning of biomass may follow a strongly heritable pattern, while showing some plasticity mediated by the rooting environment.

For the plant organs examined, as well as for dimensional parameters such as root collar and stem diameter (Appendix Tables H13 and H14), the gravel culture experiment produced much lower biomass accumulation levels than the soil composite progeny test, although both were run for a similar period of time. The apparent inability of the test to permit uninhibited free growth may mean the test has been unable to resolve seed source differences and treatment effects. The cause-effect relationships between growth parameters and treatments is difficult to resolve, as pH, Al, Fe, Ca and Mg were all varied simultaneously. Clearer interpretations may be possible with alteration of one rooting environment feature at a time. Foliage of some seedlings was analyzed to determine the cause of poor performance. Good- and poor-performing plants from each region were selected for this assay, but the results, tabled in Appendix I, offered no firm trends with which stunting could be explained.

In a third progeny test to be discussed, aluminum response of seedlings was evaluated in a hydroponics experiment.

Table IV.21 Gravel culture progeny test; ratio of above- to below-ground dry weight. 'Calcareous', 'near-neutral' 'acidic' treatments are referred to as 'H', 'W' and 'K', respectively.

a. seed source site averages

SEED SOURCE SITE	Site Average	Above-/below-ground dry weight TREATMENT		
		H	W	K
HA	3.55	3.76	4.01	2.80
HB	3.79	4.20	3.61	3.52
HC	3.72	3.70	4.43	2.89
WA	3.21	3.11	3.31	3.23
WB	3.15	3.25	3.50	2.54
WC	3.13	3.19	3.35	2.85
KA	3.14	3.24	3.14	2.90
KB	3.26	3.25	3.78	2.47
KC	3.23	3.07	3.73	2.80

b. seed source region averages

		Above-/below-ground dry weight TREATMENT			
		H	W	K	
SEED SOURCE REGION	H	3.85	4.10	3.03	3.67
	W	3.18	3.39	2.91	3.16
	K	3.18	3.54	2.72	3.20
	Ave	3.40	3.68	2.90	3.35

Significance of F values:
Region main effect - .000
Treatment main effect - .000
Region x treatment interaction - .521

D. Hydroponics Progeny Test

D.1. Dry matter accumulation

As expected, biomass averages were significantly greater in the aluminum-free treatment than in the solutions with aluminum. For total, root and above-ground dry weights, the significance of the treatment effect is described by F values of .005, .029 and .004, respectively. The presence of aluminum at 5.6 ppm appears to induce some degree of inhibition in all seed source regions, although the magnitude varies among sites within regions and among regions.

Total and above-ground dry weights (Table IV.22 to IV.24) are marked by a lack of seed source effect at the $p=0.05$ level. This apparent insignificance may be attributed to the variable response of sites within regions. Continuing a previously noted pattern, seedlings from the WB site had the lowest overall rank, while those of the WA site were predominantly superior. The Hinton and Keg River seed source sites were equally diverse, with overall averages as high as 1179 and 1106 mg for HC and KC sites and as low as 1022 and 974 mg/plant for HB and KB total seedling weight. Values for sites within regions were widely separated in the total and above-ground parameters. In the above-ground data, several sites (HA, WB and KB) were distinguished by a reversal of the expected trend towards a higher biomass value in the absence of aluminum. The extent of such differences lends insignificance to the overall total dry weight of the Hinton seed source regions being the lowest in the Al treatment and highest in the non-Al treatment, although a cautious note can be made as to the region means reflecting relative tolerance to the moderately low amount of aluminum in solution.

The dominance of seedlings from the Hinton region in performance ranking on the non-Al solution may reaffirm the observed superiority of Hinton-origin plants, as described in the results of other tests. In the presence of aluminum, the competitive advantage of Hinton seedlings was reduced and, the high rank of the region lost. Although the differences among regions were small, the Hinton seed source region had the lowest average on the Al treatment,

Table IV.22 Hydroponic progeny test; total dry weight. Aluminum and non-aluminum treatments are referred to as 'Al' and 'non-Al', respectively.

a. seed source site averages

SEED SOURCE SITE	Site Average	Seedling total dry weight (mg) TREATMENT	
		Al	non-Al
HA	1054	1159	949
HB	1023	699	1347
HC	1179	1085	1273
WA	1179	1152	1206
WB	816	831	800
WC	1150	1096	1204
KA	1072	980	1164
KB	974	1012	936
KC	1107	960	1253

b. seed source region averages

		Seedling total dry weight (mg) TREATMENT		
		Al	non-Al	Ave
SEED SOURCE AREA	H	981	1189	1085
	W	1027	1070	1048
	K	984	1118	1051
	Ave	997	1126	1061

Significance of F values:
Region main effect - .757
Treatment main effect - .005
Region x treatment interaction - .330

Table IV.23 Hydroponic progeny test; above-ground dry weight. Aluminum and non-aluminum treatments are referred to as 'Al' and 'non-Al', respectively.

a. seed source site averages

SEED SOURCE SITE	Site Average	Seedling above-ground dry weight (mg) TREATMENT	
		Al	non-Al
HA	937	1047	827
HB	911	624	1197
HC	1028	954	1102
WA	1040	1027	1053
WB	722	735	710
WC	1017	953	1080
KA	931	851	1012
KB	849	872	826
KC	940	813	1067

b. seed source region averages

		Seedling above-ground dry weight (mg) TREATMENT		
		Al	non-Al	Ave
SEED SOURCE REGION	H	875	1042	958
	W	905	948	926
	K	845	968	907
	Ave	875	986	930

Significance of F values:
Region main effect - .546
Treatment main effect - .004
Region x treatment main effect - .412

Table IV.24 Hydroponic progeny test; leaf dry weight. Aluminum and non-aluminum treatments are referred to as 'Al' and 'non-Al', respectively.

a. seed source site averages

SEED SOURCE SITE	Site Average	Seedling leaf dry weight (mg) TREATMENT	
		Al	non-Al
HA	752	833	671
HB	736	499	973
HC	833	792	874
WA	834	812	857
WB	567	587	546
WC	800	738	863
KA	726	663	789
KB	670	685	654
KC	749	633	865

b. seed source region averages

		Seedling leaf dry weight (mg) TREATMENT		
		Al	non-Al	Ave
SEED SOURCE REGION	H	708	839	773
	W	712	755	734
	K	660	769	715
	Ave	693	788	741

Significance of F values:
Region main effect - .286
Treatment main effect - .002
Region x treatment main effect - .481

perhaps indicating a marked susceptibility to Al. Stem and leaf production in this provenance is considerably more sensitive to Al, while the seedlings from the less calcareous native habitats are more resistant to growth inhibition.

The random selection of only two families to represent each site in the test was a necessary decision confining the size of this test. Given the variable responses seen, it may have been desirable to observe several more families per site to add assurance to the main effect of seed source. One site from each of the three regions exhibited unexpected response to the presence of aluminum. The HA, WB and KB site production was greater on the Al treatment than on the non-Al treatment. This behavior would suggest a physiologic insensitivity to Al at the nominal concentration.

As in total dry weight data, site specific responses for root dry weight data (Table IV.25) have a few anomalies. WB, WC and KB site growth was patterned to the reverse of the other sites, as root production is greater in the presence of Al. Despite this feature, the seed source effect in the data was dramatic. In the root dry weight data of Table IV.25, there is a faint interaction that is not statistically significant at $p=0.05$. In the absence of Al, Hinton seedling production was near that of Keg River seedlings and Whitecourt was slightly inferior. However, the presence of Al caused a reduction in root biomass in all regions, the greatest degree of inhibition being in the Hinton seed sources. Overall, the sensitivity of Hinton seedlings to this heavy metal seems larger than for the other two regions; this may be indicative of a negative interaction between Hinton seedling root systems and the presence of a moderately low amount of Al in solution. Whitecourt seedlings showed relative indifference to the presence of Al. Averages are nearly equal for both treatments. Before concluding the profoundness of this trend, the generally poor growth of the WB site should be considered. The erratic behavior of this site and the WC site, perhaps by the inclusion of two less-than-representative families in the test, may serve to mask any real features contained in the gene pool of the Whitecourt region.

Table IV.25 Hydroponic progeny test; root dry weight. Aluminum and non-aluminum treatments are referred to as 'Al' and 'non-Al', respectively.

a. seed source site averages

SEED SOURCE SITE	Site Average	Seedling root dry weight (mg) TREATMENT	
		Al	non-Al
HA	117	112	123
HB	112	75	149
HC	151	131	171
WA	139	125	153
WB	93	96	90
WC	133	143	124
KA	141	130	152
KB	125	140	110
KC	167	147	186

b. seed source region averages

		Seedling root dry weight (mg) TREATMENT		
		Al	non-Al	Ave
SEED SOURCE REGION	H	106	148	127
	W	121	122	122
	K	139	149	144
	Ave	122	141	131

Significance of F values:
Region main effect - .060
treatment main effect - .029
Region x treatment interaction - .101

Expressing biomass measurements as an above- to below-ground ratio, the seed source effect is seen to be significant at the $p=0.05$ level, whereas the treatment effect is negligible. The results described on Table IV.26 reveal how the collective ratio of the Keg River seedlings was the lowest for all treatments; root production per unit of above-ground biomass was high for the Keg River seedlings. Particularly in the Al treatment, those seedlings may be regarded as being more capable of maintaining root growth. The Keg River seed sources may be adapted to greater amounts of ionic forms of Al in parental soils, thus were able to sustain more root growth in the presence of aluminum. In a converse argument, Hinton and Whitecourt seedlings appeared more efficient in generating above ground biomass per unit amount of root production. Whatever the interpretation, comparison of non-Al treatment ratio finds an increasing trend for Hinton and Whitecourt seedlings versus one that declines for Keg River seedlings.

Branch length increments (Table IV.27) were assessed after five weeks of seedling establishment in the pots and at the time of harvest. The treatment effect is not significant at $p=0.05$, but is at $p=0.10$. The seed source effect is not significant at either level. As before, several sites displayed increased values in the presence of Al. While the HA, WA, WB and KB sites responded in this way, there was an apparent decrease in seed source region averages on the Al treatment. The Keg River seed source had the highest value for the non-Al solution and maintained a high value on the Al solution. The Hinton average dropped much more markedly on the Al treatment, indicating stronger sensitivity to aluminum.

Branch number and branch length data had been expected to align closely with leaf dry weight data because branch lengths represent the extent of surfaces wherein needles are initiated. Hinton seed sources were ranked highest on the non-Al treatment and the Keg River seed region placed lowest on the Al treatment, a trend opposing that seen in the branch length increment data. Also notable was the inhibition of leaf biomass accumulation in Keg River sites on the Al solution. Recalling the above- to below-ground ratio of this seed source on the treatment, dry matter partitioning appeared to involve a shift in emphasis away from

Table IV.26 Hydroponic progeny test; ratio of above- to below-ground dry weight. Aluminum and non-aluminum treatments are referred to as 'Al' and 'non-Al', respectively.

a. seed source site averages

SEED SOURCE SITE	Site Average	Above-/below-ground dry weight TREATMENT	
		Al	non-Al
HA	10.2	11.5	9.0
HB	11.5	12.0	11.0
HC	9.2	9.2	9.1
WA	11.3	13.5	9.1
WB	11.7	10.5	12.9
WC	13.0	13.6	12.5
KA	9.5	9.3	9.7
KB	9.7	8.1	11.3
KC	7.9	8.9	6.8

b. seed source region averages

		Above-/below-ground dry weight TREATMENT		
		Al	non-Al	Ave
SEED SOURCE REGION	H	10.9	9.7	10.3
	W	12.5	11.5	12.0
	K	8.7	9.3	9.0
	Ave	10.7	10.2	10.4

Significance of F values:
Region main effect - .601
Treatment main effect - .397
Region x treatment interaction - .496

Table IV.27 Hydroponic progeny test; branch length increments. Aluminum and non-aluminum treatments are referred to as 'Al' and 'non-Al', respectively.

a. seed source site averages

SEED SOURCE SITE	Site Average	Branch length increment (mm) TREATMENT	
		Al	non-Al
HA	78	89	67
HB	86	56	116
HC	89	79	98
WA	107	112	102
WB	68	70	67
WC	103	95	110
KA	100	94	105
KB	94	87	81
KC	102	92	113

b. seed source region averages

		Branch length increments TREATMENT		
		Al	non-Al	Ave
SEED SOURCE REGION	H	75	94	84
	W	92	93	93
	K	91	99	95
	Ave	86	96	91

Significance of F values:
Region main effect - .200
Treatment main effect - .067
Region x treatment interaction - .340

above-ground parts to the roots. Hinton and Whitecourt seed sources, on the other hand, maintained high ratios and since root production rates are lower, leaf production acts as a stronger sink for photosynthates.

D.2. Seedling dimensions

From Table IV.28, stem height appeared to be greater for Keg River seedlings than for Hinton seedlings on both treatments. Keg River seedling stem height, being highest overall, is evidence for the population allocating more photosynthate into the bole of the plant. Hinton seedlings, especially on the Al treatment, proportioned considerably less into this compartment. This may partially account for the emphasis of the seed source in maintaining large leaf weights.

Table IV.28 Hydroponic progeny test; stem height increments. Aluminum and non-aluminum treatments are referred to as 'Al' and 'non-Al', respectively.

a. seed source site averages

SEED SOURCE SITE	Site Average	Stem height increment (mm) TREATMENT	
		Al	non-Al
HA	32	32	32
HB	31	22	41
HC	36	34	37
WA	36	38	34
WB	26	27	25
WC	39	39	40
KA	38	32	43
KB	32	36	29
KC	42	34	50

b. seed source region averages

		Stem height increments(mm) TREATMENT		
		Al	non-Al	Ave
SEED SOURCE REGION	H	29	37	33
	W	35	33	34
	K	34	41	37
	Ave	33	37	35

Significance of F values:
Region main effect - .156
Treatment main effect - .024
Region x treatment interaction - .084

E. Comparison of Progeny Tests

For each of the dry weight components, seed source averages from the soil composite experiment and the hydroponics experiment are compared on a relative basis, in two different fashions. Firstly, seed source performance is graphed relative to the treatment where productivity is greatest for that seed source. On another graph, the relative productivity of the various seed sources is plotted for each treatment.

Figures IV.3 to IV.5 illustrate the principles of such relative assessments of treatment productivity with the total, above-ground and leaf dry weight data. For the soil composite test, maximal dry weight for each seed source region was attained on the Keg River soil composite. On the other soils, growth was less than this Keg River maximum by a certain percentage of reduction. On the Hinton soil composite, the reduction was greatest for all populations, although collectively, the Hinton seed source had the least relative decrease in total dry weight when growth was compared to the level achieved on the Keg River soil. The difference between the Keg River and Whitecourt seed regions was minor. The Hinton-region seedlings maintain nearly 55% of their maximal expression, while the other two seed source regions are below 50% of the maximum performance attained on the acid soil. On the more acidic Whitecourt treatment, Whitecourt and Keg River above-ground dry weights responded to levels nearer their Keg River maxima. Above-ground and leaf parameters also displayed the patterns of biomass decline with increasing alkalinity. There was a greatest reduction in the traits in the acid-origin provenances grown on the calcareous treatment. On the Hinton soil composite, the reduction is greatest for all seed source regions, although the Hinton seed sources have the least relative decrease in total dry weight when growth is compared to the level achieved on the Keg River soil. Although the difference between the Keg River and Whitecourt seed regions is minor, the acid-originating provenance has the greatest relative decrease. This may indicate the extent to which the calcareous-originating provenance is most adapted to the non-sterilized calcareous soil composite than its counterparts from more acidic parental habitats.

Figure IV.3. Total dry weight; relative treatment productivity.
For each seed source, productivity is plotted relative to the treatment on which total dry weight was maximal.

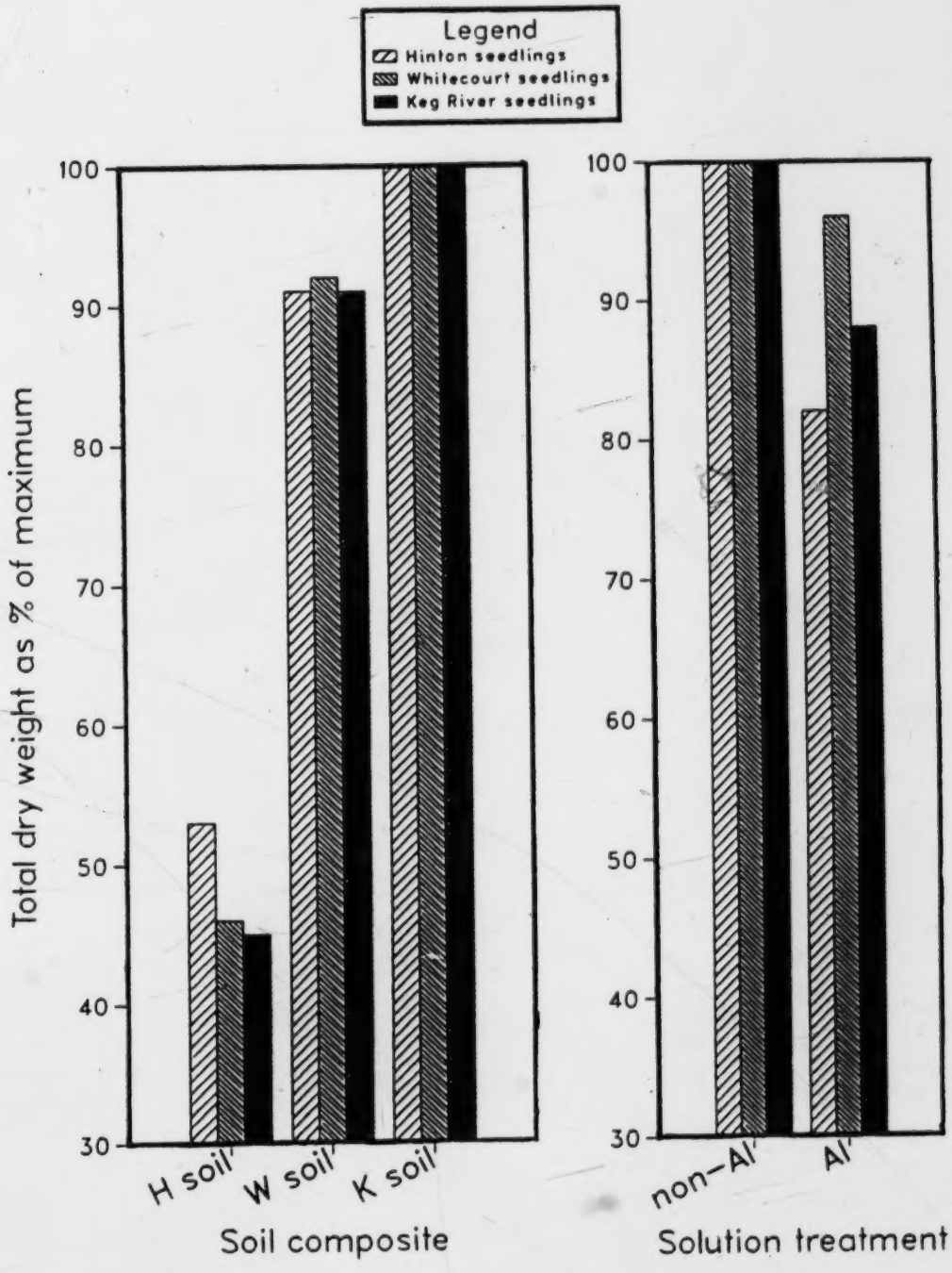


Figure IV.4. Above-ground dry weight; relative treatment productivity.
For each seed source, productivity is plotted relative to the treatment on which above-ground dry weight was maximal.

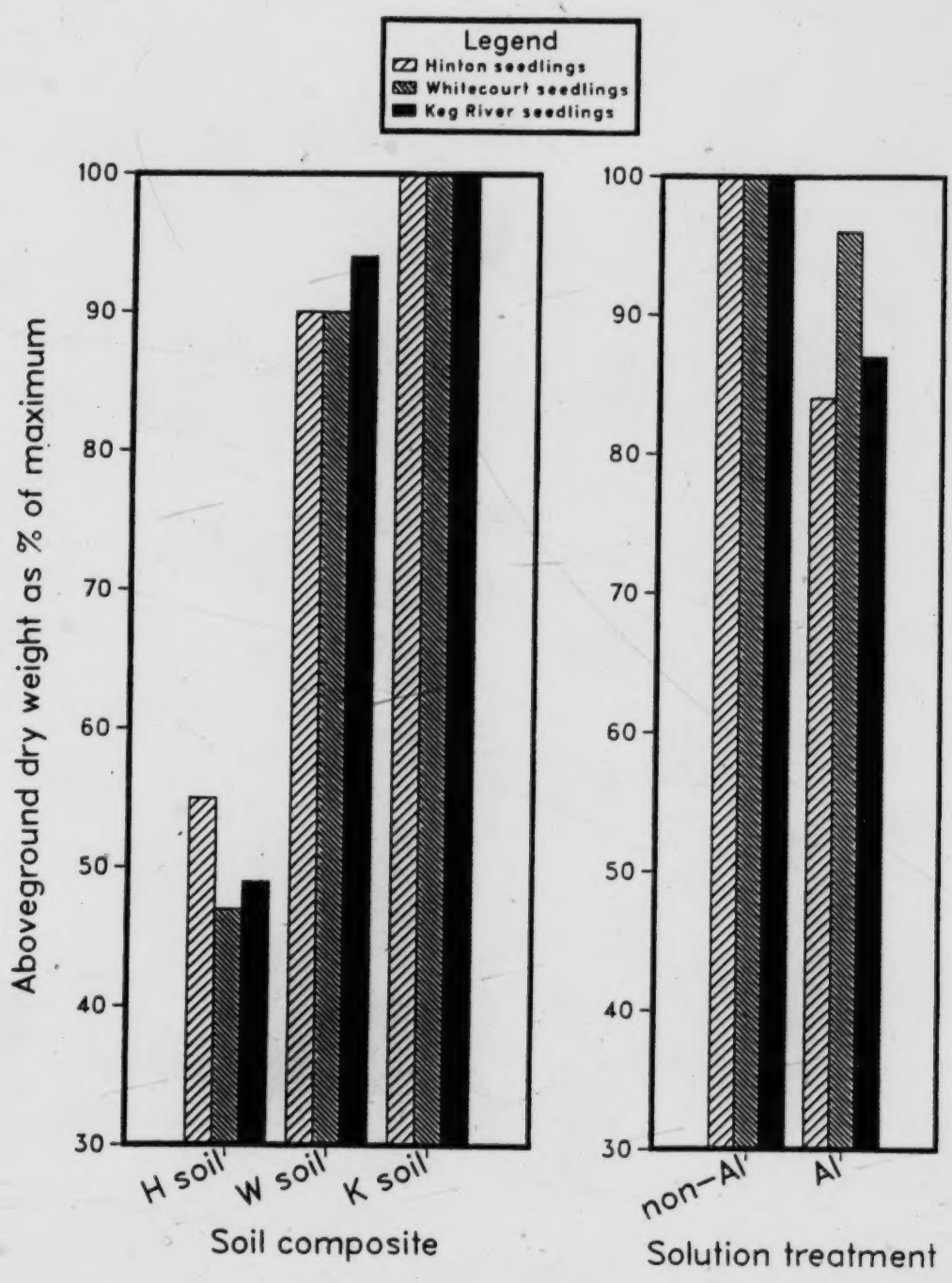
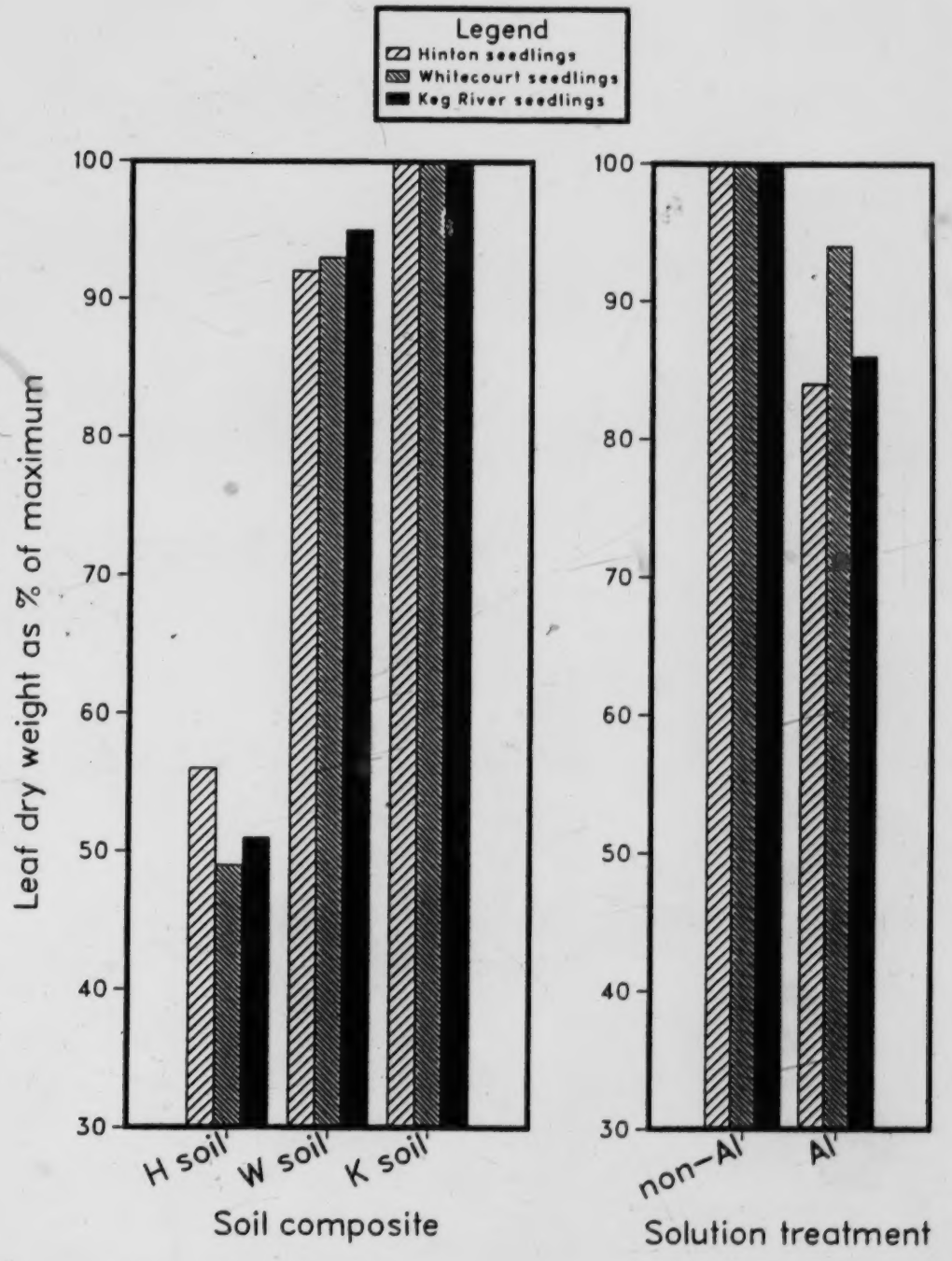


Figure IV.5. Leaf dry weight; relative treatment productivity.
For each seed source, productivity is plotted relative to the treatment on which leaf dry weight was maximal.



Calcifuges (acid-origin provenances) of *Agrostis setaea* have a higher-affinity calcium uptake mechanism than calcicoles (Lauchi 1975). The two types may differ in the nature of membrane-bound ATP-ases involved in ion transport. It is possible that, on the calcareous soil, calcifuges may absorb quantities of Ca that lead to undesirable cationic ratios in root tissues. Lauchi generalized calcifuges as having shoot K/Ca ratios on the order of 100:1, as opposed to ratios of 1:1 in calcicoles. This was due to selective ion uptake differences in roots. Clark (1976) agreed that differing capacities to selectively absorb minerals may exist, perhaps under the control of 2 or more genes. Further, this Ca selectivity may be related to the degree of Al tolerance and may be equated with high mineral use efficiency (the ability to accumulate high dry matter production per unit of element taken up). The Whitecourt and Keg River seed sources may possess such highly Ca-selective ion transport pathways since their productivity was more inhibited in the Ca-rich Hinton soil.

Hydroponic test results show that the non-Al treatment supported the most biomass accumulation for Hinton and Keg River seedlings. Whitecourt seedlings were least sensitive to Al in solution. Compared to this ceiling of development, Hinton seedlings, on the Al solution, were most severely inhibited, It appears, then, that the adaptive superiority of the Hinton seedlings, as seen in the soil composite progeny test may be dependent on soil microorganisms; processes operating at the rhizosphere markedly influence the productivity potential of the plant. The data leave the notion that aluminum in solution affects growth of Hinton seedlings more than the seedlings derived from acidic soils. With mycorrhizal and other possible biological influences absent, the Hinton seedlings may be very sensitive to the acidic environments.

Those provenances not developed on calcareous soil may have acquired differential tolerance to Al by several mechanisms. Mugwira *et al* (1976) observed high rhizosphere pH values associated with Al-tolerant wheats (*Triticum aestivum* L.). This attribute, they posulated, was incurred by any or all of the following activities:

1. H^+ release resultant from excess cation over anion absorption,

2. minimized release and hydrolysis of CO_2,
3. minimized release of H^+ from COOH of polygalacturonic acid residues associated with acid membranes, and
4. minimized secretion of H^+ from root-associated microorganisms.

Root sterility would result in the elimination of the fourth point as a probable operative feature in this experiment. The second point may be more probable, given the reduction in root respiration in response to Al in the rooting environment of Al-tolerant *Sorghun bicolor* plants (Cambraia *et al* 1983).

While the remaining three points may be part of the acid-originating provenances' adaptive strategy, their benefits in terms of mediating rooting environment pH are minimized in the hydroponic progeny test, where pH was below 5.0 throughout the experiment. Realization of tolerance potential would have to have been achieved by other means.

To add to Mugwira's work, studies of *Picea abies* and *Fagus sylvatica* Al tolerance led Van Preeg *et al* (1985) to believe a preference of NO_3^- over NH_4^+ as the N source was involved. This fact was reaffirmed by the report of low nitrate reductase and restricted NO_3^--utilization abilities of such plants as *Betula verrucosa* from acid soils (Foy *et al* 1978). A high rate of ammonium uptake would cause a pH decrease, leading to acidification of the rhizosphere. Aluminum tolerance in the wheat cultivars studied by Foy and co-workers was correlated to the ability to use nitrate efficiently in the presence of ammonium. The mechanism of plant tolerance to Al may not be one of pH alteration, but may be expressed through metabolic selectivity as described.

Other theories may be considered; Al absorption may be reduced by exclusion mechanisms or it may be detoxified after it has been absorbed. Al-tolerant *Sorghum bicolor* plants were found to absorb more Al in free root spaces (Cambraia *et al* 1983). This was achieved by the level of root organic acids being 55% higher in tolerant plants than in those that were intolerant. Trans-aconitate and malate were two of the organic acids subject to accumulation in an Al-laced environment. Brown (1977) has shown that some plant species

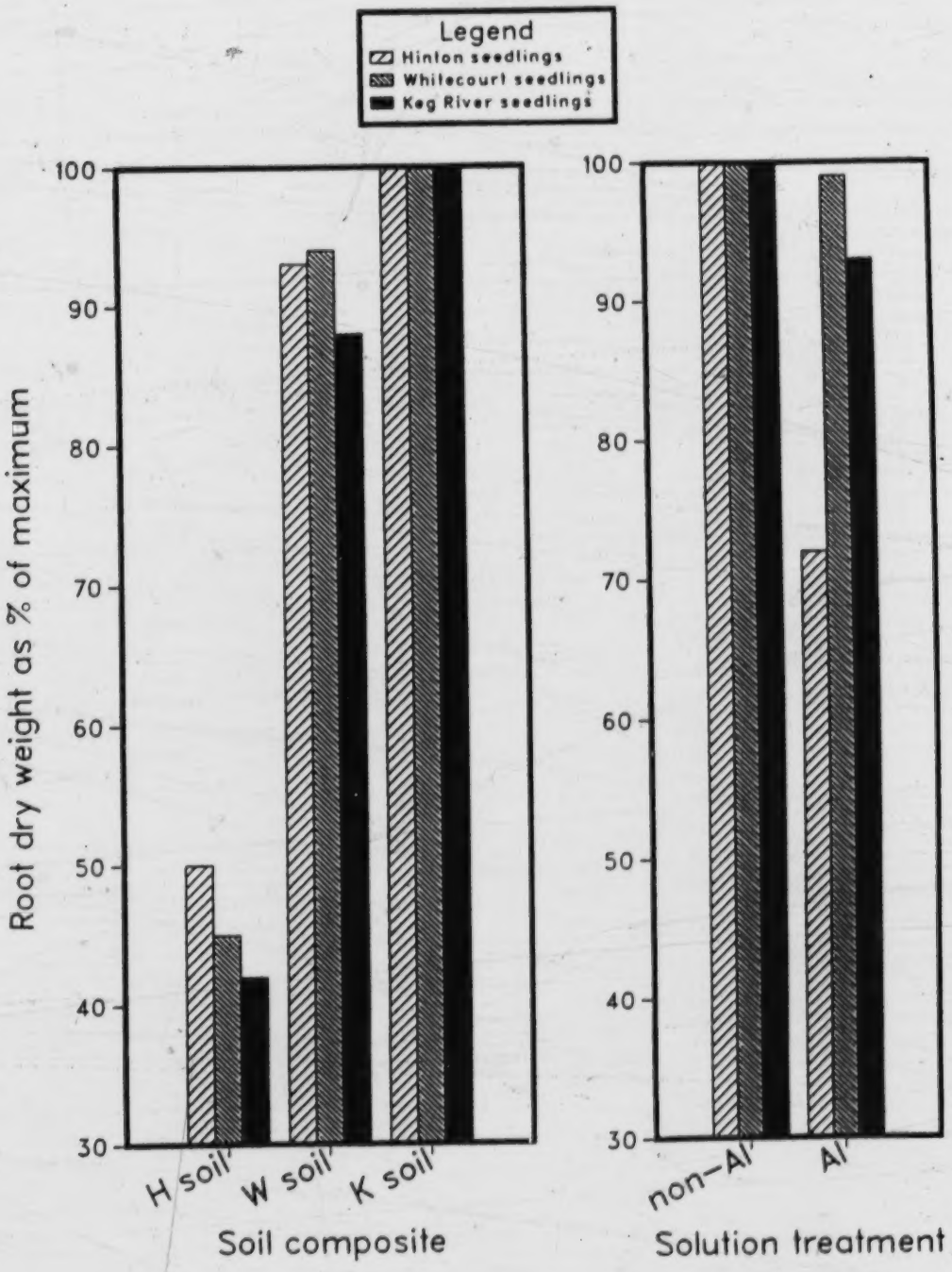
may respond to Fe by exuding low molecular weight organic acids and that this property is variable among genotypes. Iron tolerance then, may be described as the ability to chelate and inactivate the metal ion in the rhizosphere. Aluminum tolerance mediated by such a scheme may be possible.

In the hydroponic progeny test, the Al-tolerant Whitecourt and Keg River provenances may have possessed lower rates of CO_2 production, increased relative uptake of nitrate and enhanced organic acid production. As these plant properties were not assessed, the contribution they may have had towards a reduction in Al absorption is not known. In addition, foliage and root analyses were not performed to examine possible differences in Al activity in Al-tolerant and sensitive plants.

Bollard (1983) observed that translocation of Al from roots to tops is greater in Al-sensitive plants. Tolerance may be due to precipitation of Al in apoplastic spaces in roots, a result of high production of free OH^- groups in cell walls of tolerant plants (Foy *et al* 1978). This would constitute a genetic control of Al-susceptability. Foy also stated that, as part of the genetic specificity to plant reactions to Al, chemical and ionic exchange properties of pecto-cellulose cell walls may offer some differences in absorption and localization of Al in roots. Bollard also noted that levels of Ca in foliage of sensitive plants was lower than that in tolerant plants in the presence of Al and uptake of P in the presence of Al was greater in tolerant plants. Had foliage nutrient levels and total elemental concentrations been determined, it would have been possible to identify nutrient uptake rates as causes of the observed growth differences between seed sources.

Root dry weight data can be expressed in a similar fashion to depict the relative behavior of the seed source regions. In Figure IV.6, the relative productivity of the seed sources for each treatment are shown. As with total dry weight data, greatest root production was characteristic of the Keg River soil composite with a progressive decrease in Whitecourt and Hinton treatments. On parental soil, Hinton seedlings average only 50% of their level on the Keg River treatment, yet Whitecourt and Keg River seedlings were slightly more reduced—

Figure IV.6. Root dry weight; relative treatment productivity.
For each seed source, productivity is plotted relative to the treatment on which root dry weight was maximal.



to approximately 45 and 42 %, respectively. On the Whitecourt soil, Keg River seedlings were most reduced (88% of maximum), where Hinton and Whitecourt plants maintained levels of 92 and 94 %. Clearly, the Keg River seed is more specifically adapted to biological and chemical conditions imposed on the parental Keg River soil type; higher specificity causes a sharper decline in root production on the Whitecourt and Keg River treatments. By comparison, Hinton seedlings are most resilient on Hinton soil and yet, are also capable of high rates of root biomass accumulation on the more acidic conditions represented by the other two soils. On the basis of such comparisons, the Hinton seed could be described as retaining broader adaptability.

In the hydroponic test, greatest root production was seen in the absence of aluminum. With Al present, Hinton seedling root production dropped most steeply, to 71% of the maximum. Whitecourt and Keg River seedlings remained relatively high at 99 and 93 %, respectively. Those seed sources whose parental habitats are more acidic seemed to have acquired greater insensitivity to the forms of Al in solution.

Figures IV.7 to IV.10 depict the relative seedling total, above-ground and leaf dry weights for the three regions. In the soil composite test, Hinton seed was superior to its counterparts on each treatment. This predomination is particularly dramatic on the Keg River soil composite, where overall, Hinton seed performance was approximately 17% greater than that of Whitecourt or Keg River seed. Whitecourt and Keg River exhibited similar seedling growth on all soils.

One may infer the existence of a broad adaptability strategy in the Hinton gene pool, whereby growth is relatively high regardless of soil chemical conditions, given the presence of natural soil biological influences. In terms of above-ground biomass, the Keg River seedlings appear to be inferior on all soil types. This poor Keg River ranking, particularly on the parental Keg River soil, suggests an ingrained strategy, perhaps with lower above-ground biomass accumulation rates encouraging optimal root production.

On the non-Al solution of the hydroponic test, the superiority of Hinton seed persisted, albeit not to the same degree. The competitive advantage of Hinton seedlings over Whitecourt

Figure IV.7. Total dry weight; relative seed source productivity.
For each treatment, productivity is plotted relative to the seed source whose total dry weight was maximal.

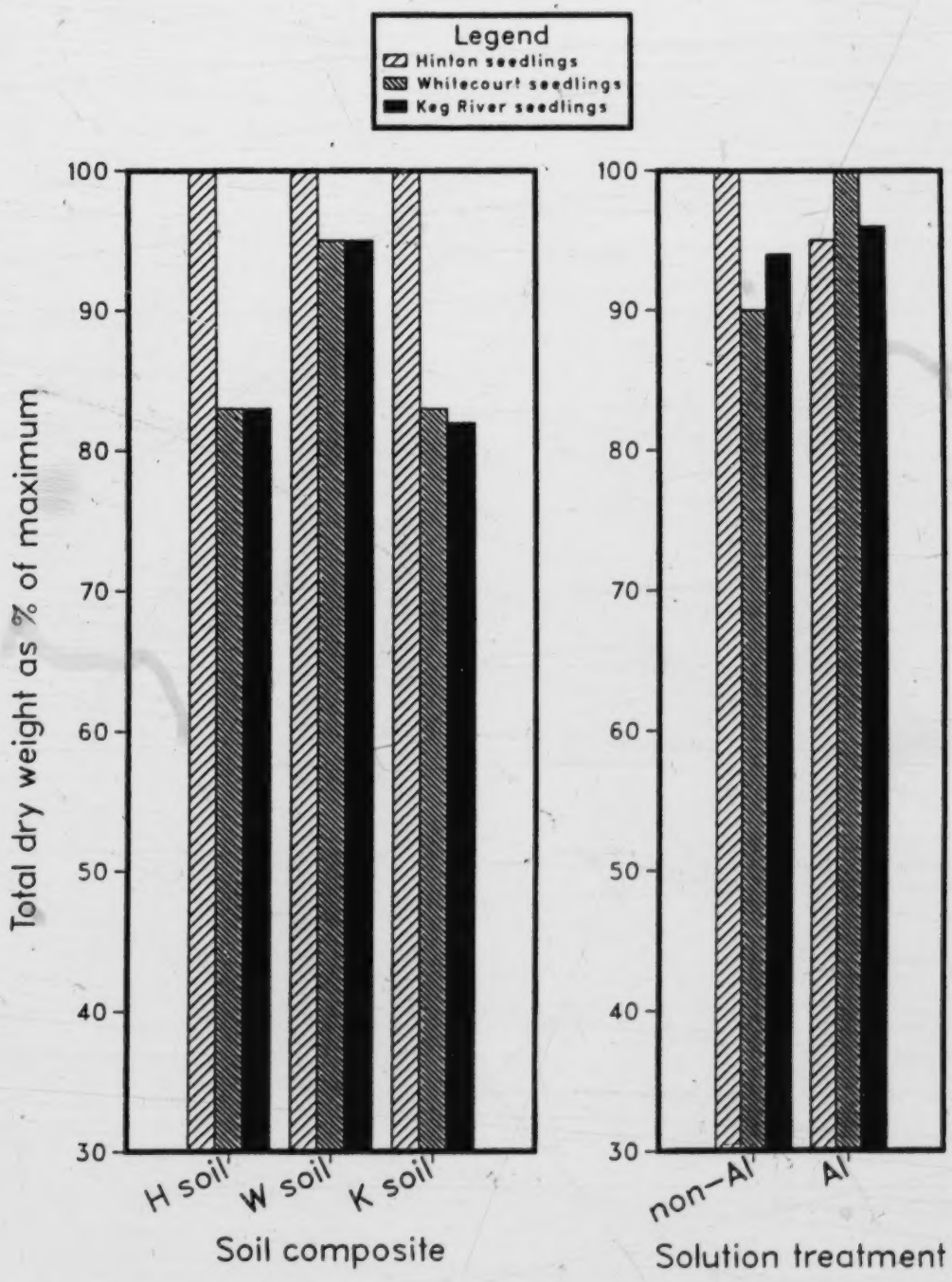


Figure IV.8. Above-ground dry weight; relative seed source productivity.
For each treatment, productivity is plotted relative to the seed source whose above-ground dry weight was maximal.

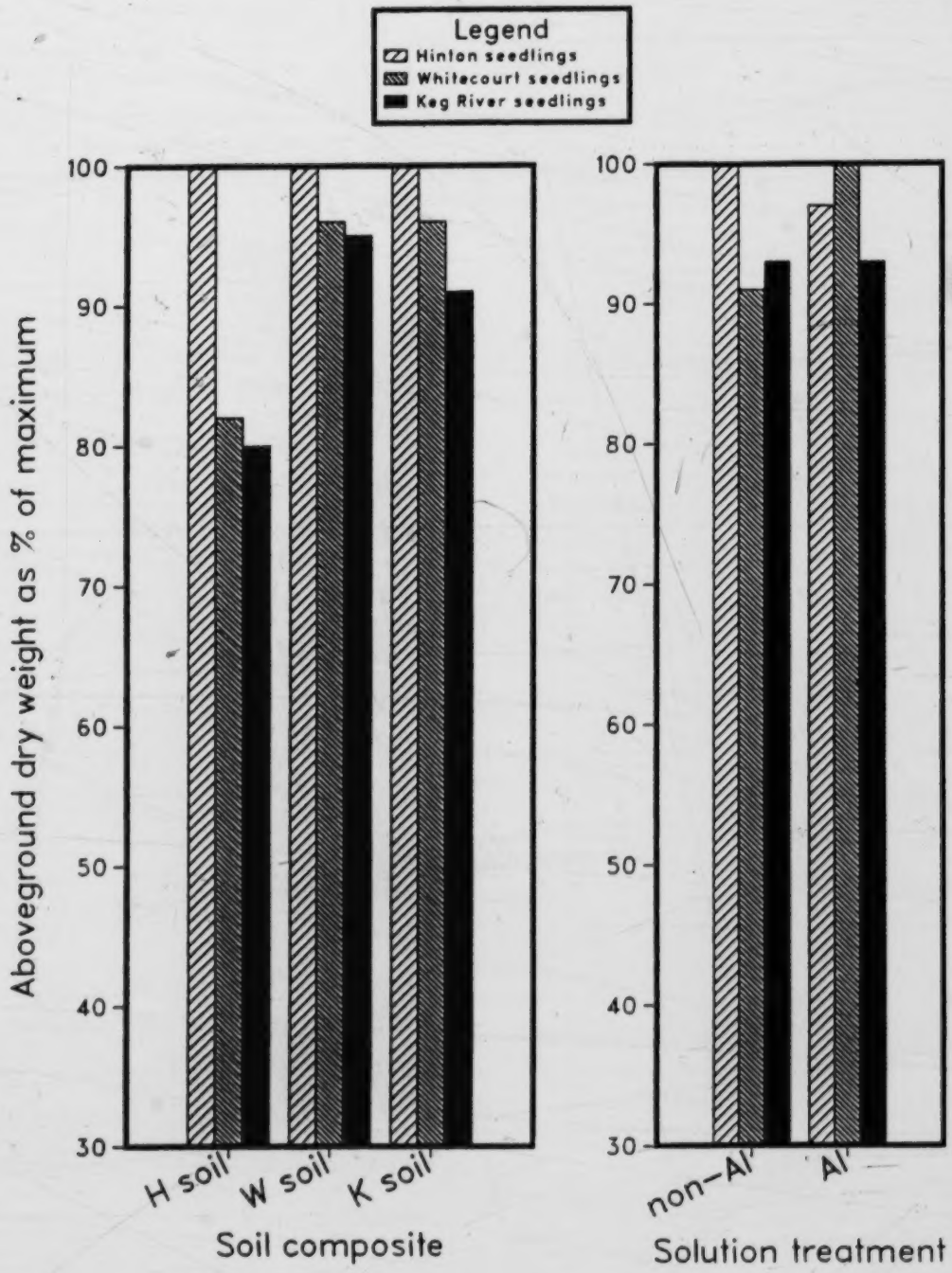
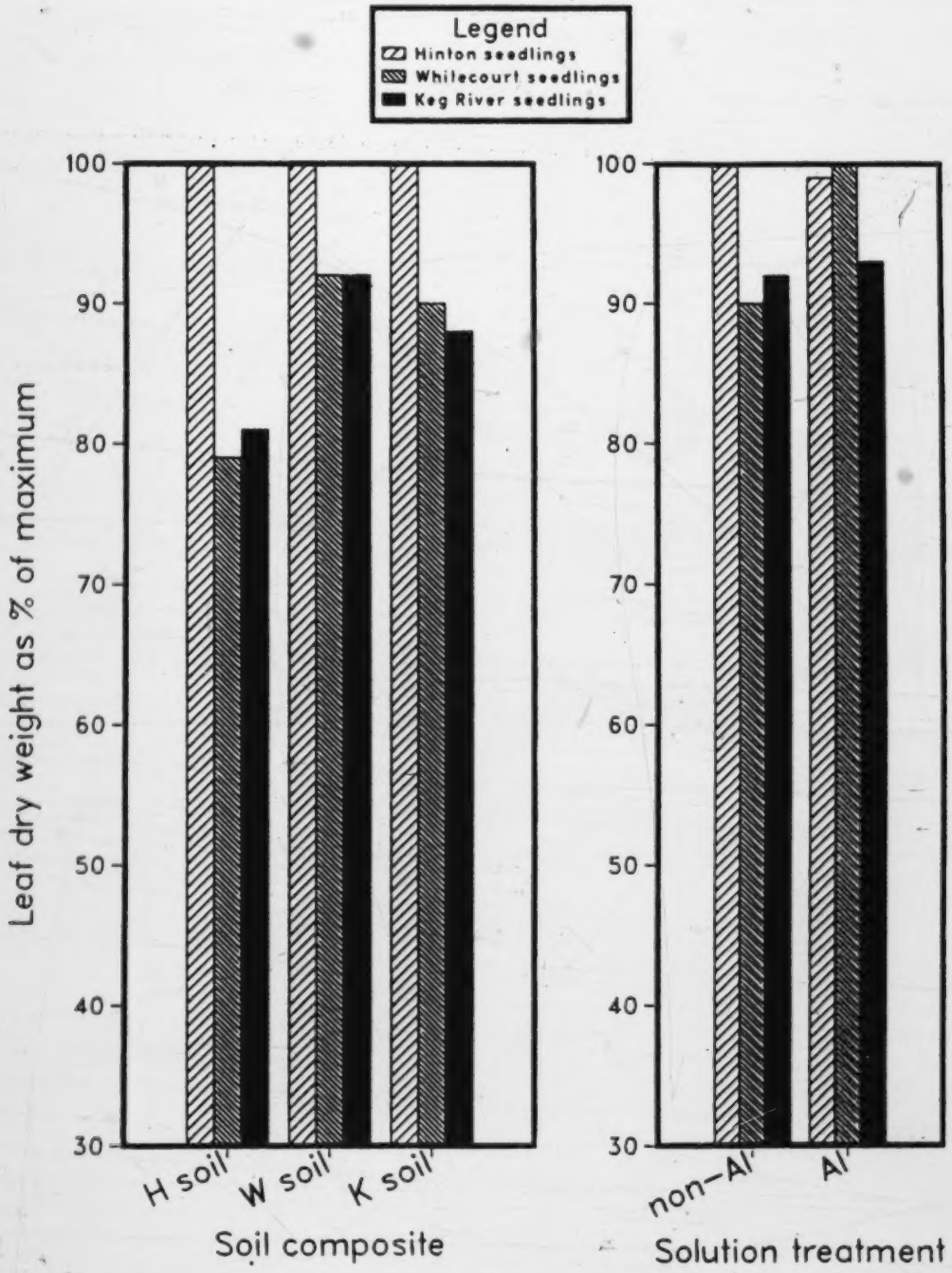


Figure IV.9. Leaf dry weight; relative seed source productivity.
For each treatment, productivity is plotted relative to the seed source whose leaf dry weight was maximal.



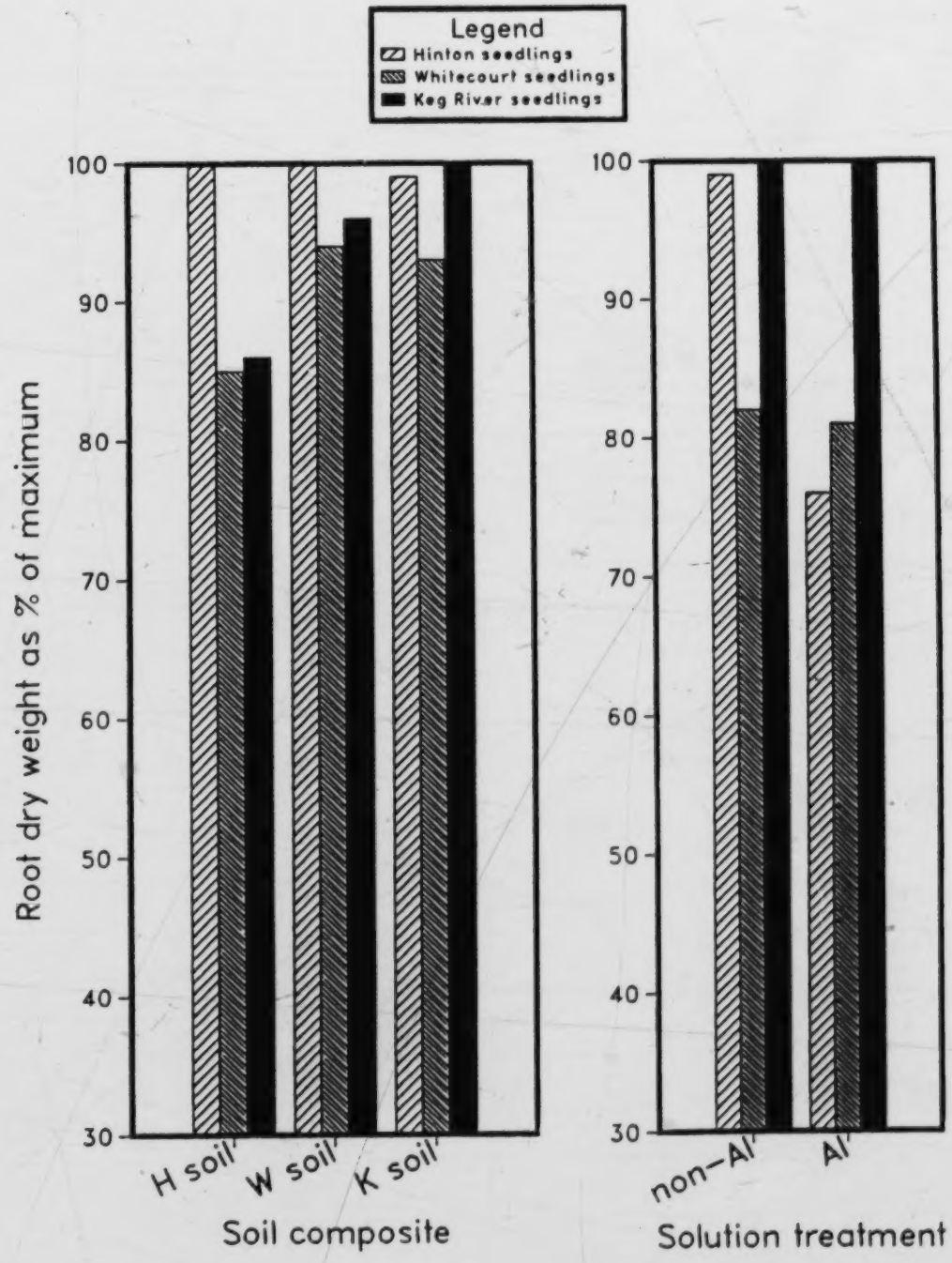
seedlings was lost only upon the addition of ionic forms of aluminum into solution.

The Hinton seedling averages exceeded those of the Keg River in above-ground and leaf compartments in both experiments. The notion of inherent physiological constraints on biomass partitioning may be partially involved in an answer to the cause for such consistent ranking. Hinton seedlings are capable of greater biomass increments, even when root growth is severely inhibited, as on the Al solution. Hence they may possess a strategy lending to competitive success. Emphasis may be placed on leaf initiation, even at the expense of other plant parts. On a regional basis, Hinton seedlings appeared least capable of maintaining previously-achieved levels of biomass production. Seedings of the Whitecourt region appeared more capable than those of the Keg River region in tolerating this condition. Again, this may be an artifact relating to the relatively poor growth of one of the Whitecourt seed source sites. WB seedlings may be inferior in physiological capabilities and may express random reactions to the treatments applied.

Figure IV.10 reveals how the seed source root dry weights are ranked within any one treatment. In the soil composite test, greatest root production occurred in the Hinton seedlings on Hinton and Whitecourt soils. On Keg River soil, the maximum was shared by Hinton and Keg River seedlings, indistinguishable at 99 and 100%. The high rank of Hinton seedlings, most marked on Hinton soil, is lost or dampened on the more acidic soils and hence, one may conclude that there is some degree of adaptive specificity with regard to root response to the three rooting environments. Hinton seedlings grew well on their parental soil, while Keg River seedlings responded most positively to acidic conditions on the parental soil.

On the non-Al hydroponic solution, extent of root development of Hinton and Keg River seedlings was similar, with that from Whitecourt apparently being most deficient. The ranking abruptly shifted in the presence of aluminum. Here, the Keg River seed source region appeared to be most superior; root production in Hinton seedlings in the presence of Al is only 76% that of Keg River. The results reaffirm the positive adaptation of the roots of Keg River seedlings to free forms of aluminum. The more calcareous the soil of the seed origin, the

Figure IV.10. Root dry weight; relative seed source productivity.
For each treatment, productivity is plotted relative to the seed source whose root dry weight was maxmial.



greater the negative reaction becomes. With no soil biological aides to mediate or modify root metabolism or soil ionic forms of Al, the Hinton seedlings were distinctly sensitive to the Al solution culture.

Figures IV.11 and IV.12 express the relative ratios of above- to below-ground dry weight. The information indicates maintenance of lower ratios in Keg River plants on the acidic soil composite and on the Al treatment. Meanwhile the same seed source ranked highest on the calcareous Hinton soil and the non-Al solution. Hinton seedlings behaved similarly on the soil composites, however on the Al solution, a high ratio is observed. Whitecourt seedlings tended to increase ratios to a maximum from calcareous to acidic soils and increasing also from non-Al to Al treatments.

In terms of nutrient allocation strategy, the Keg River seedlings proportion more carbon into root biomass as conditions become more acidic or as Al appears in solution. Presumably, seedlings of the Keg River region were exhibiting root adaptations for coping with soil acidity. For Hinton seedlings, decreasing ratios with decreasing soil pH also reflected root tolerance to acidic conditions; however, the Hinton response was dependent upon the presence of some unidentified soil biological components, as in the soil composite progeny test. With the presence of Al in the hydroponic test, root production was severely restricted. The pattern displayed in Whitecourt seedlings was the reverse of the Hinton trend.

Figure IV.11. Above- to below-ground dry weight ratio; relative treatment productivity. For each seed source, productivity is plotted relative to the treatment on which the ratio was the highest.

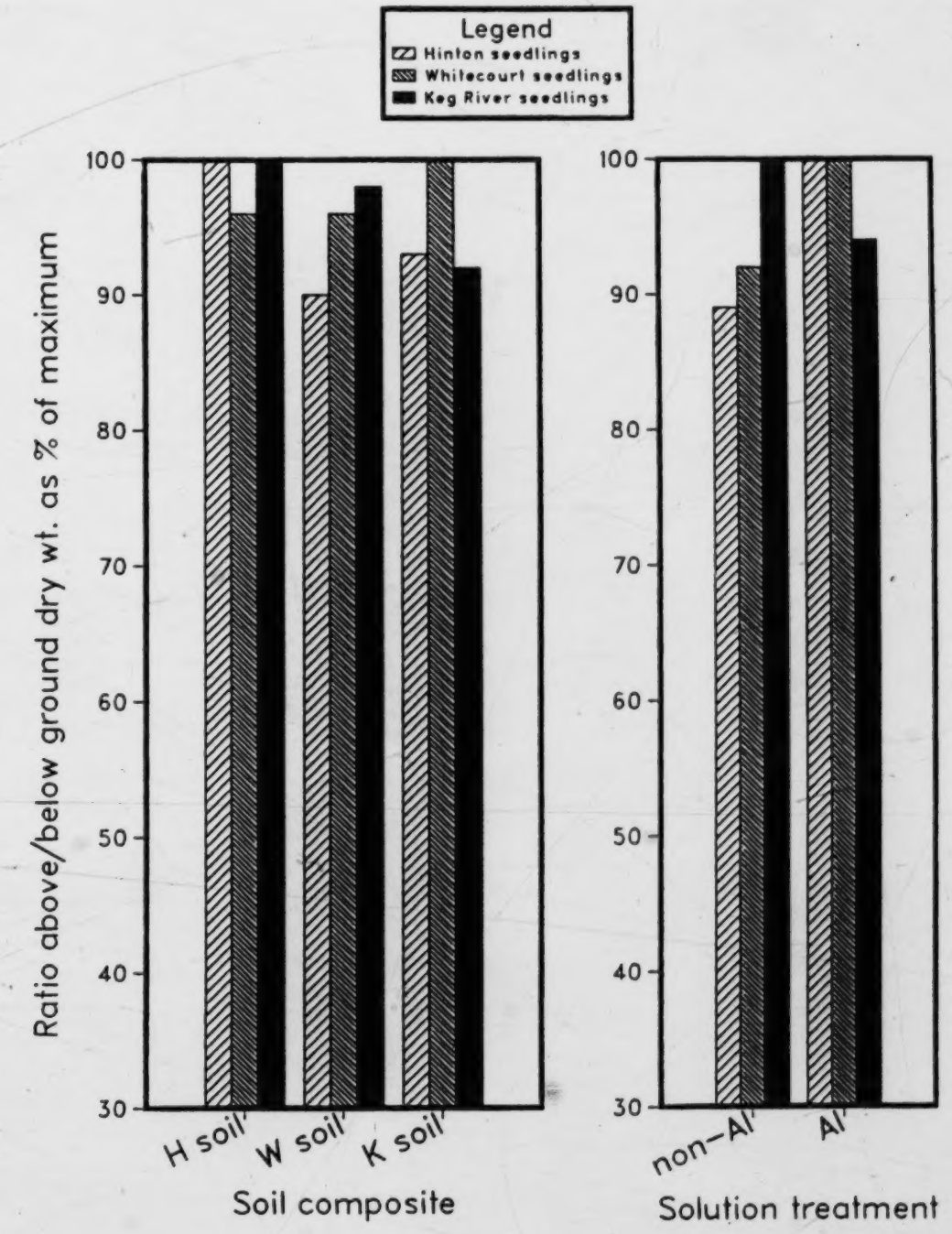
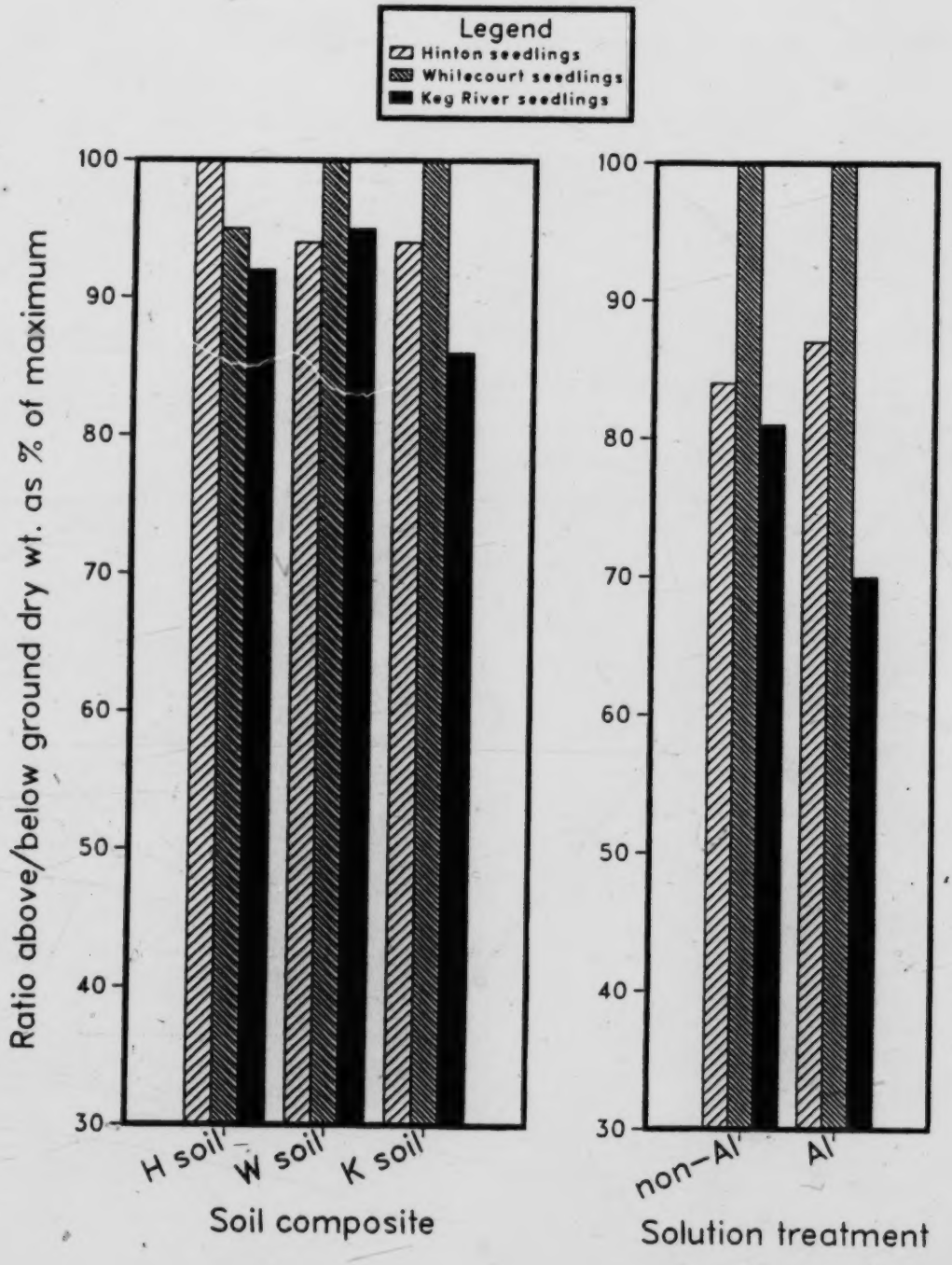


Figure IV.12. Above- to below-ground dry weight ratio; relative seed source productivity. For each treatment, productivity is plotted relative to the seed source whose ratio was the highest.



F. Dry Matter Partitioning Patterns

Triaxial diagrams, such as those generated by Wacquant and Bouab (1984), are used to illustrate site differences in the relative dry weights of the root, shoot and stem and branch plant compartments. The results for the soil composite and hydroponic progeny tests are illustrated in Figures IV.13 and IV.14. In Figure IV.13, soil composite progeny test results are shown. The morphological assessments made here are important as comparisons of dry matter partitioning. As an index of organic assimilate distribution patterns, each allows the visualization of differences among the provenances tested. The position of the Hinton seed source region in the hydroponic progeny test reflects the negative response of Hinton root systems to Al in solution. Keg River and Whitecourt seedlings exhibited a drop in leaf weight but not root dry weight when subjected to Al. For these latter seed source regions, the presence of Al induced a more neutral response in root dry weight whereas for Hinton provenance, the response was distinctly negative. The triaxial diagram in Figure IV.14 indicates how sensitive this calcareous-origin provenance is to the presence of Al in the absence of mycorrhizal infections.

The diagram in Figure IV.13 reveals regional-based differences in the allocation of biomass to leaves and roots in the acidic and calcareous soils. Keg River seedlings had proportionately more carbon in root systems on both soils and Hinton seedlings show a marked emphasis on leaf production. These features of the provenances were noted previously.

As Molina and Chamard (1983) noted, host species respond differently to inoculation with fungi, indicating differences in allocation of host photosynthate from tops to roots. Typically, mycorrhizal roots, with greater respiration needs than non-mycorrhizal roots, are stronger sinks for assimilated carbon (Smith 1980). On the Keg River soil, efficiency of ion uptake may be enhanced by proper performance of the root-fungal association. Root meristems, being closest to nutrient supply, recieve more nutrients than shoot meristems or leaf initials in high nutrient soil conditions (Chapin 1980). Sutcliff (1975) warned that nutrient allocation patterns may shift over the life of the plant, as such phenomena as hormonal

Figure IV.13. Triaxial diagrams; soil composite progeny test. For each seed source region, stem and branch, leaf and root dry weight averages are expressed as a percent of the total dry weight average. The angles of indicators along side each percentage mark denote the angle at which the plant component is graphed.

Legend:

▲ H seedlings on the K soil composite
● W seedlings on the K soil composite
■ K seedlings on the K soil composite
△ H seedlings on the H soil composite
○ W seedlings on the H soil composite
□ K seedlings on the H soil composite

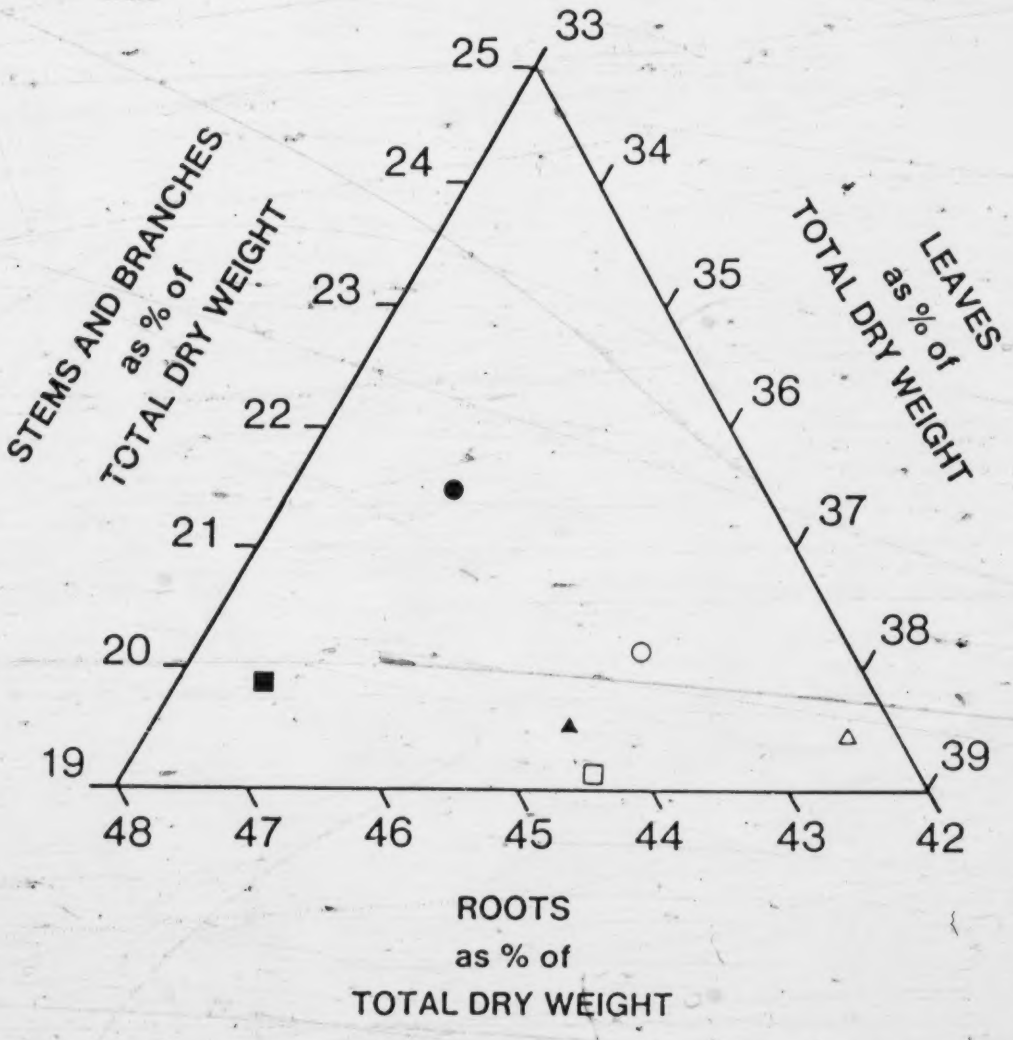
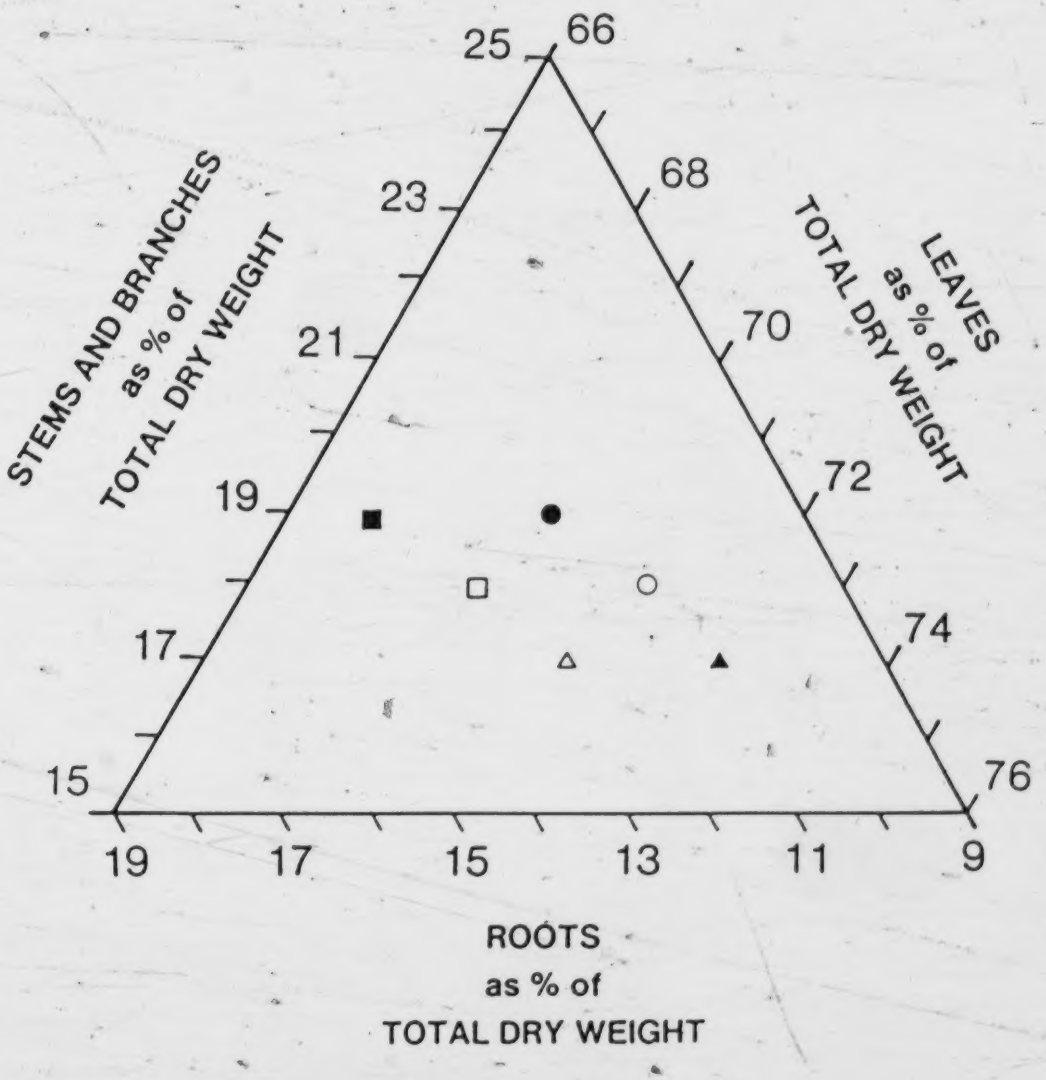


Figure IV.14. Triaxial diagram; hydroponic progeny test. For each seed source region, stem and branch, leaf and root dry weight averages are expressed as a percentage of the total dry weight average. The angles of indicators along side each percentage mark denote the angle at which the plant component is graphed.

Legend:

▲ H seedlings on the Al solution
● W seedlings on the Al solution
■ K seedlings on the Al solution
△ H seedlings on the non-Al solution
○ W seedlings on the non-Al solution
□ K seedlings on the non-Al solution



activities and changes induced by flowering periodicity are involved in carbon allocation and ion redistribution.

G. Relative Root Tolerance

The following table depicts the relative root production of the three seed source regions in the Hinton vs. Keg River soils of the soil composite progeny test and the Al and non-Al solutions of the hydroponic progeny test. In the soil composite test, root production on Hinton is divided by that on Keg River; and in the hydroponic test, growth on Al is divided by the non-Al averages. For both tests, the root tolerance index is an expression of the relative inhibition of root biomass accumulation in the most deleterious treatment compared to levels in the most advantageous treatment. Because the frame of reference shifts between the progeny tests, no comparisons can be made across them.

Table IV.29. Relative root tolerance of the seed source regions.
For soil composite progeny test data, growth on Hinton soil is given relative to growth on Keg River soil. For hydroponic progeny test data, growth on aluminum solution is given relative to growth on non-aluminum.

RELATIVE ROOT TOLERANCE		
Seed source region	Soil composite progeny test	Hydroponic progeny test
H	.500	.719
W	.454	.990
K	.424	.937

Collectively, the Keg River seed source was more inhibited in terms of root production on the Hinton soil than the other seed sources. Similarly, the Hinton seed sources were more inhibited in the presence of aluminum in solution. There may be a broad adaptability pattern existing in the Hinton seedlings when mycorrhizae are present. To the minor degree expressed here, root systems of Keg River seedlings may be slightly more narrowly adapted in terms of the positive response of root biomass accumulation in the presence of mycorrhizae; mycorrhizal root systems of Keg River seedlings exhibit greater sensitivity to the Hinton soil condition.

For the hydroponic progeny test, Keg River seedlings possessed greater insensitivity to the presence of Al in solution. In the absence of mycorrhiza, acidic-originating seedlings may harbor greater resilience to the soluble forms of Al in the rooting solution.

H. Regression coefficients versus mean yields

To illustrate varietal adaptation differences, Finlay and Wilkinson (1963) advocated the use of two-dimensional plots (scatter diagrams) with mean yield and regression coefficients used as coordinates. For such plots, a log of site means from each treatment is regressed on the log of the treatment mean. The resultant regression coefficient is plotted against the overall performance mean for that seed source site.

$$\log(\text{site mean}) = a + b(\log(\text{treat. mean}))$$

The scatter diagrams depict the sensitivity of the seed source sites to environmental change. They are a mathematical interpretation of the relative site performance means for the traits measured in the soil composite and hydroponics test which were displayed on appendix figures H1 to H9. Figure II.2 from Finlay and Wilkinson (1963) is used to interpret the scatter plots in figures IV.15 to IV.27. Because the individual variety means are plotted against the mean of all the variety yields, the population mean has a regression coefficient of 1.0.

The soil composite progeny test resolved the nine seed source sites into several groups. For example, the WB and KB sites possessed low mean yield in total and root dry weight, in a region of below average stability (Figures IV.15 and IV.16). The placement of WB and KB in this area which indicates their poor adaptability to all environments, stems from their below-average performance. WC was also in this region of poor general adaptability. The HC site, which held top rank in the Hinton soil and lesser grades on others, is positioned towards the area designated as specifically adapted to unfavorable environments. WA, HA and KC were relatively good seed sources, being near average or above in total dry weights in all treatments. The high mean yields shown by these sites places them in an area for varieties regarded as being well adapted to all environments.

For intermediary behavior, the seedlings of the KA site are considered to be specifically adapted to favorable environments, as their rank improved from a low on the Hinton soil to fourth lowest on Whitecourt and Keg River soil. Their position on the total dry weight scatter diagram (Figure IV.15) reflects this expected designation. HB was second highest on Hinton

Figure IV.15. Scatter diagram; total dry weight data of soil composite progeny test. Regression coefficient (b) derived from the equation

$$\log(\text{site mean}) = a + b \cdot \log(\text{treatment mean})$$

is plotted against log(site mean).

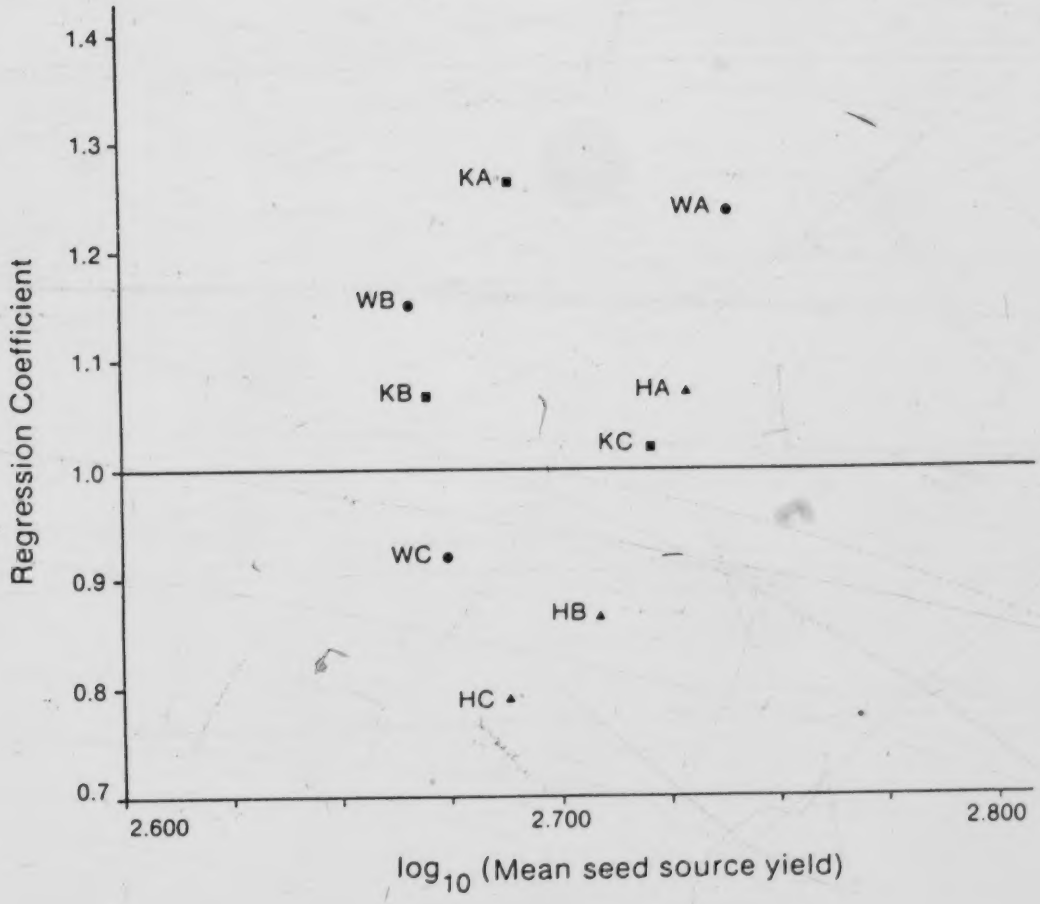
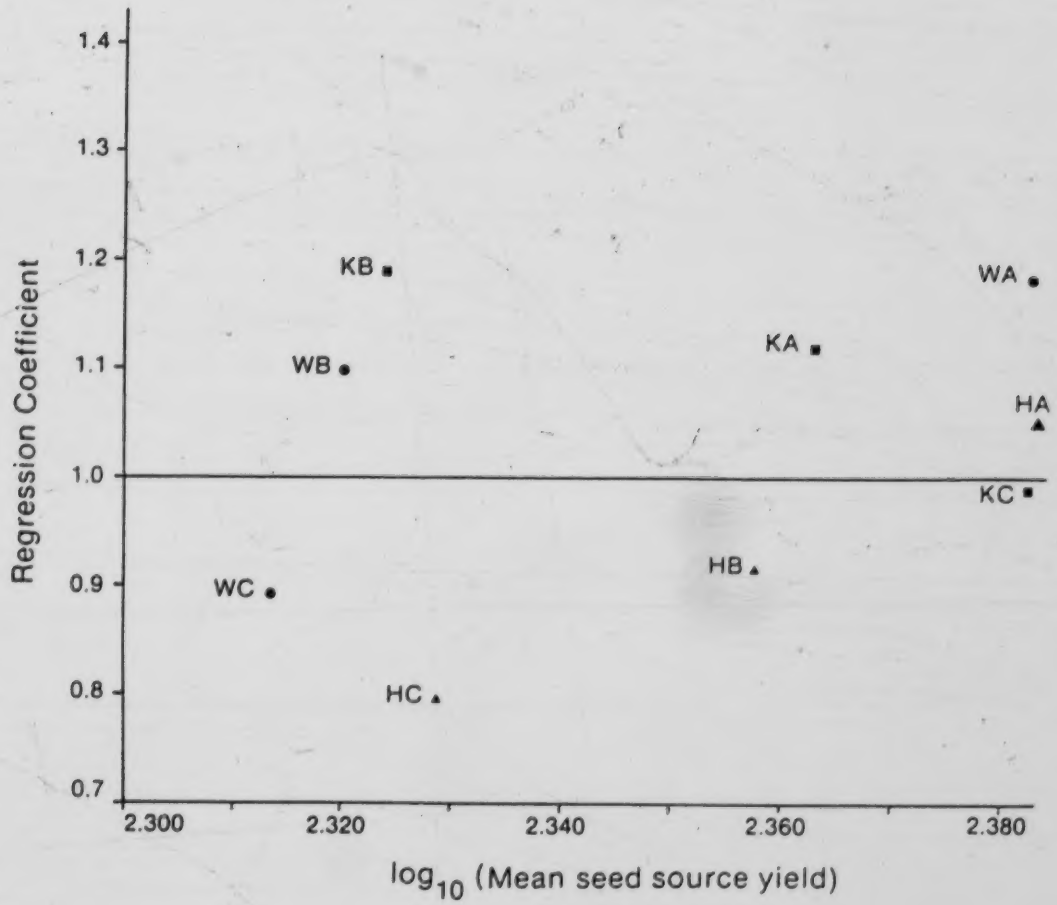


Figure IV.16. Scatter diagram; root dry weight data of soil composite progeny test. Regression coefficient (b) derived from the equation

log(site mean) = a + b · log(treatment mean) is plotted against log(site mean).



soil and placed no better than fourth on the Whitecourt and Keg River soils. Along with the HC site, the HB site tended to lie near the area designated for genotypes that are specifically adapted to unfavorable environments.

A similar basic pattern is shown for the root dry weight data of the soil composite test (Figure IV.16). Again, the WA, HA and KC sites lead in mean yield, with consistent performance implying they were well adapted to favorable environments. This region is now shared by the KA site that in terms of root production, is more broadly adapted than in total biomass accumulation. One other change for the Keg River region is the relocation of KB away from an area of poor adaptability to all environments to one denoting specific adaptability to favorable environments. This site shared the rank for lowest root production in the Hinton soil, but improved its relative standing in the more favorable Whitecourt and Keg River soils. More than in the total dry weight measurements, WC and HC seed was specifically adapted to the unfavorable Hinton soil.

The above-ground and leaf dry weight scatter diagrams for the soil composite test reflect dramatic shifts in capability of the Keg River sites (Figures IV.17 and IV.18). Where for roots KC is very broadly adaptive, it was only average in the above-ground dry weight data. The KA site was extremely narrowly adapted to favorable environments, since it is far below average on the Hinton soil. The mean yield for the KB site was equally low. By being positioned close to the treatment averages, it was designated as being poorly adapted to all environments.

WA, WB and WC remained basically unaltered from previous patterns. While WB and WC were less-than-average performers, WA appeared to be well adapted, maintaining high rank on all treatments. Hinton-region seedlings dominated in terms of adaptability on the unfavorable Hinton environment. However, since only HA is consistently above average on all treatments, that site remains in a position reflecting good general adaptability. With reasonably high yields, HB and HC are placed closer to an area with adaptations specific to unfavorable environments, in this case, the Hinton treatment.

Figure IV.17. Scatter diagram; above-ground dry weight data for the soil composite progeny test.
Regression coefficient (b) derived from the equation
log(site mean) = a + b · log(treatment mean) is plotted against log(site mean).

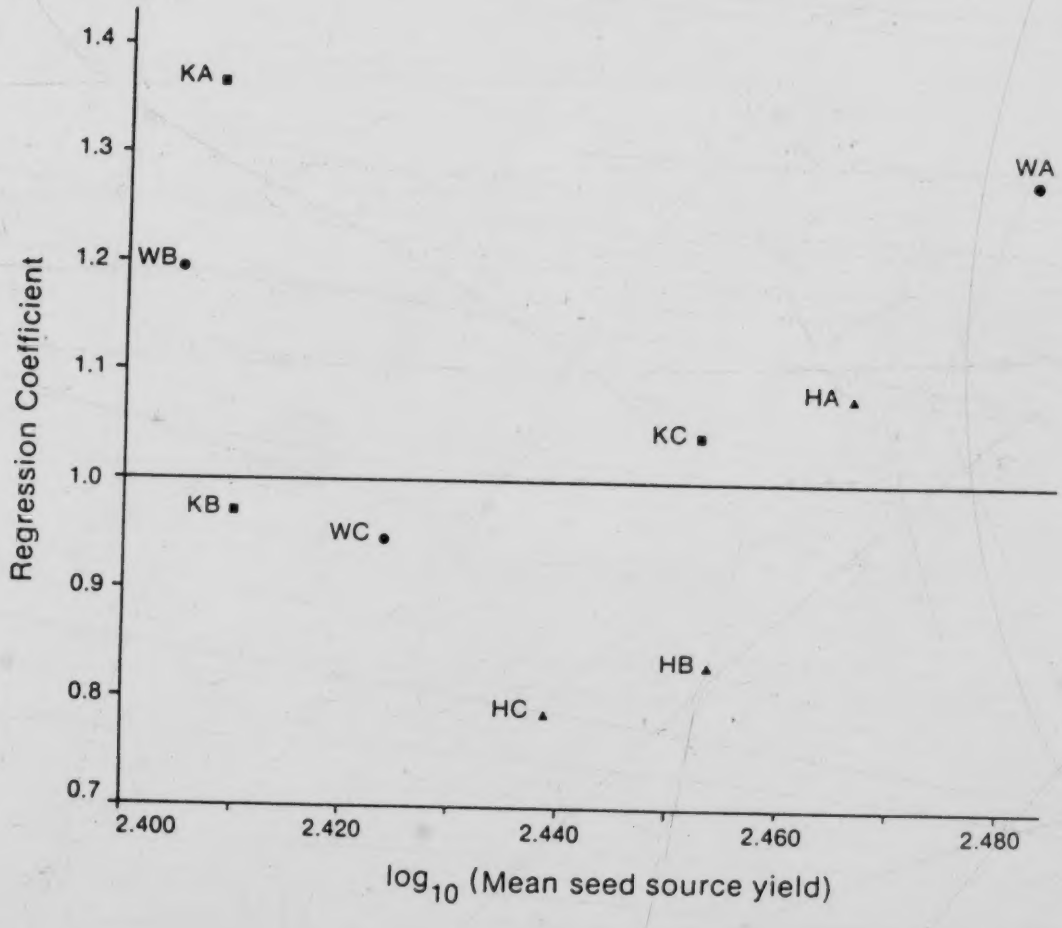
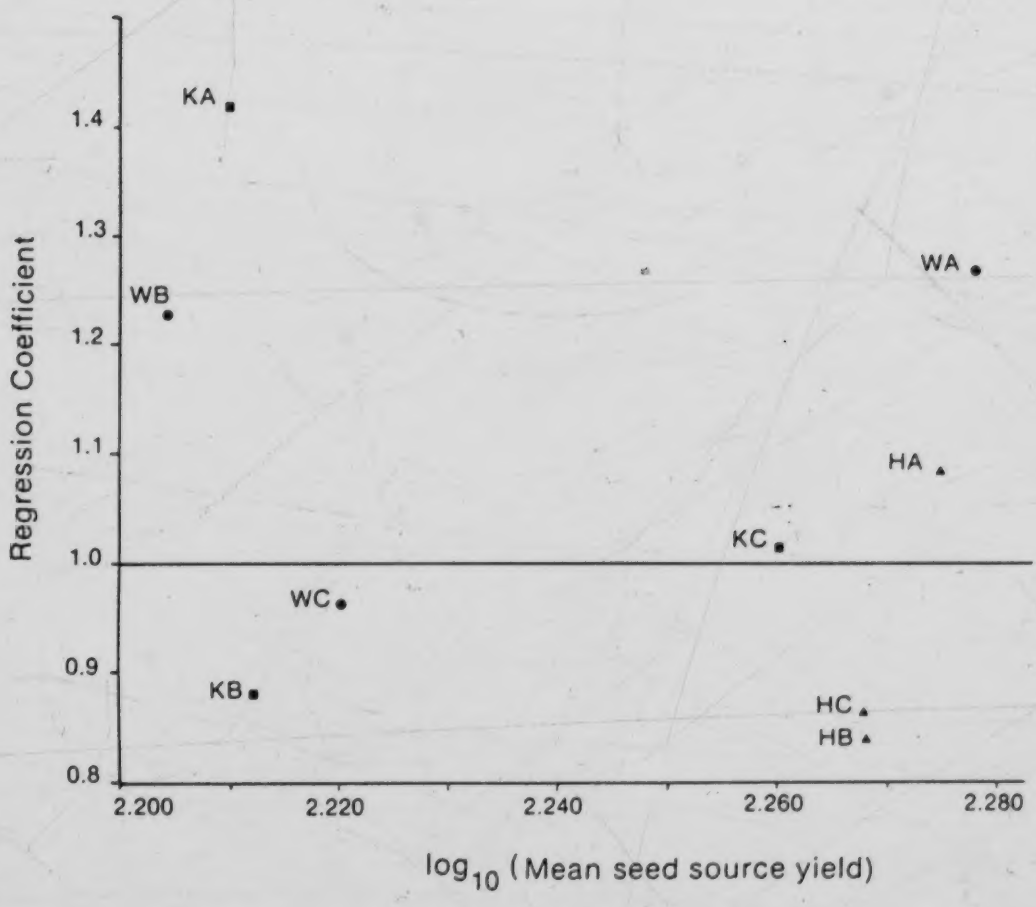


Figure IV.18. Scatter diagram; leaf dry weight data for the soil composite progeny test.
Regression coefficient (b) is derived from the equation
log(site mean) = a + b · log(treatment mean) is plotted against log(site mean).



The leaf weight index scatter diagram (Figure IV.19) accurately portrays the superior plasticity of the Hinton seed sources, sites which maintain consistently high values. This position is closely shared by the KC site, which also bears high leaf indices on all treatments. WB was far below average on Hinton soil, but with improvement on Whitecourt and Keg River treatments, it is placed in the area described for specific adaptability to favorable environments. To a much lesser extent, KB and WA rank was improved on Whitecourt and Keg River soils, but with higher yields on Hinton soil, they were not as well conditioned to growth on all soils. The rank of WC fell from the Hinton to Whitecourt to the Keg River treatments; the seed source appeared to be suited to unfavorable environments.

In referring to the scatter diagrams of hydroponic test results, it should be noted that only two treatments are used to compile the logs of seed source means and the regression coefficient. In the results of the test, variations among sites within regions are very high; therefore, further testing with increased numbers of families per site may be desirable to add validity to the trends revealed here. In Figure IV.20, response differences for total dry weight are illustrated. Most notably, the WA and WC sites were grouped along with HA, in an area representing high adaptability to all environments. Site averages were well above average on Al and non-Al treatments. At the other extreme, WB was far below average on both sites, reflecting poor adaptability. Wide ranges of adaptability occurred within the Hinton region. HA was well-adapted to both treatments whereas HB was extremely well adapted to the Al-free solution only. Marked sensitivity to Al is very unlike the behavior of HA, which, by a positive response to aluminum, was well adapted to the unfavorable environment in terms of total dry weight. Keg River seed sources were located in two distinct locales, either exhibiting relatively good growth and adaptability on both treatments (KA and KC), or responding with slight favor to the aluminum solution, hence being adapted to unfavorable conditions (KB).

The juxtaposition of sites was repeated in root dry weight data (Figure IV.21), with the exception of the HA and KB sites. Compared to seedlings of the HA site, those of the KB site were more tolerant of aluminum in terms of root production. For total dry weight and

Figure IV.19. Scatter diagram; leaf weight index data for the soil composite progeny test.
Regression coefficient (b) derived from the equation
log(site mean) = a + b · log(treatment mean) is plotted against log(site mean).

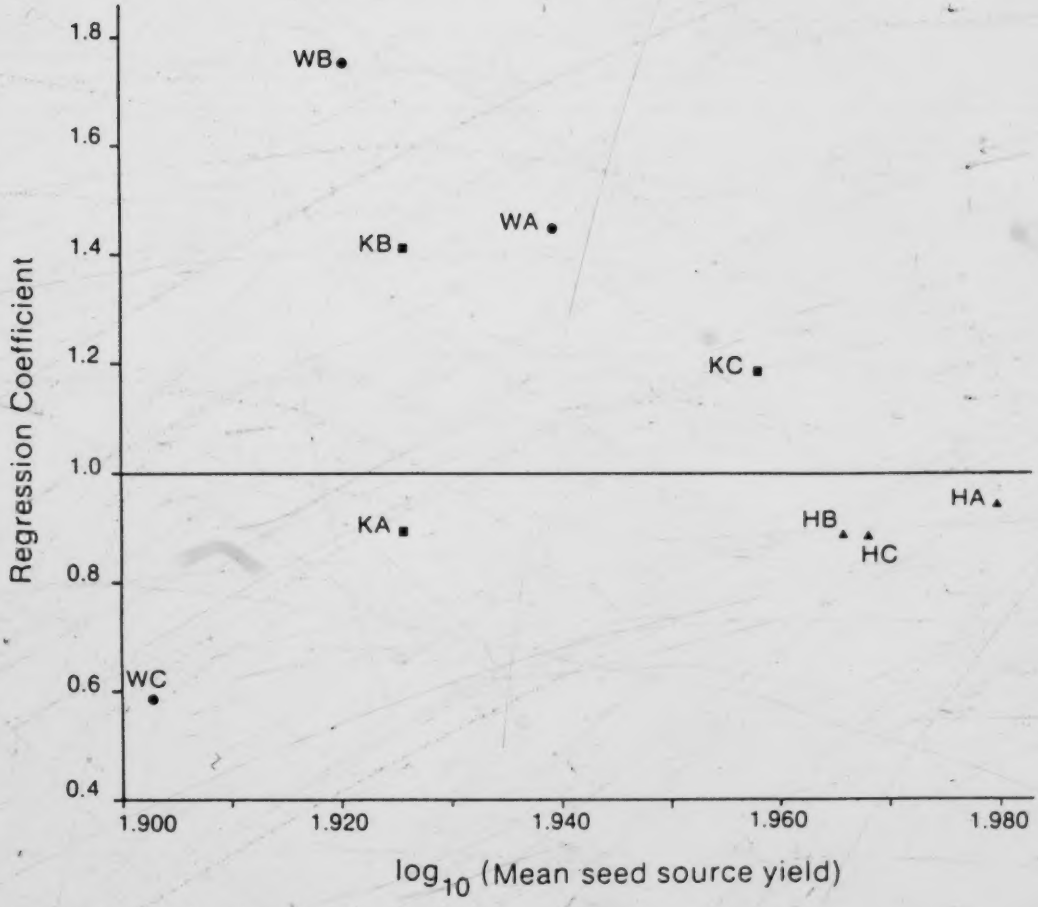


Figure IV.20. Scatter diagram; total dry weight data for the hydroponics progeny test.
Regression coefficient (b) derived from the equation
log(site mean) = a + b · log(treatment mean) is plotted against log(site mean).

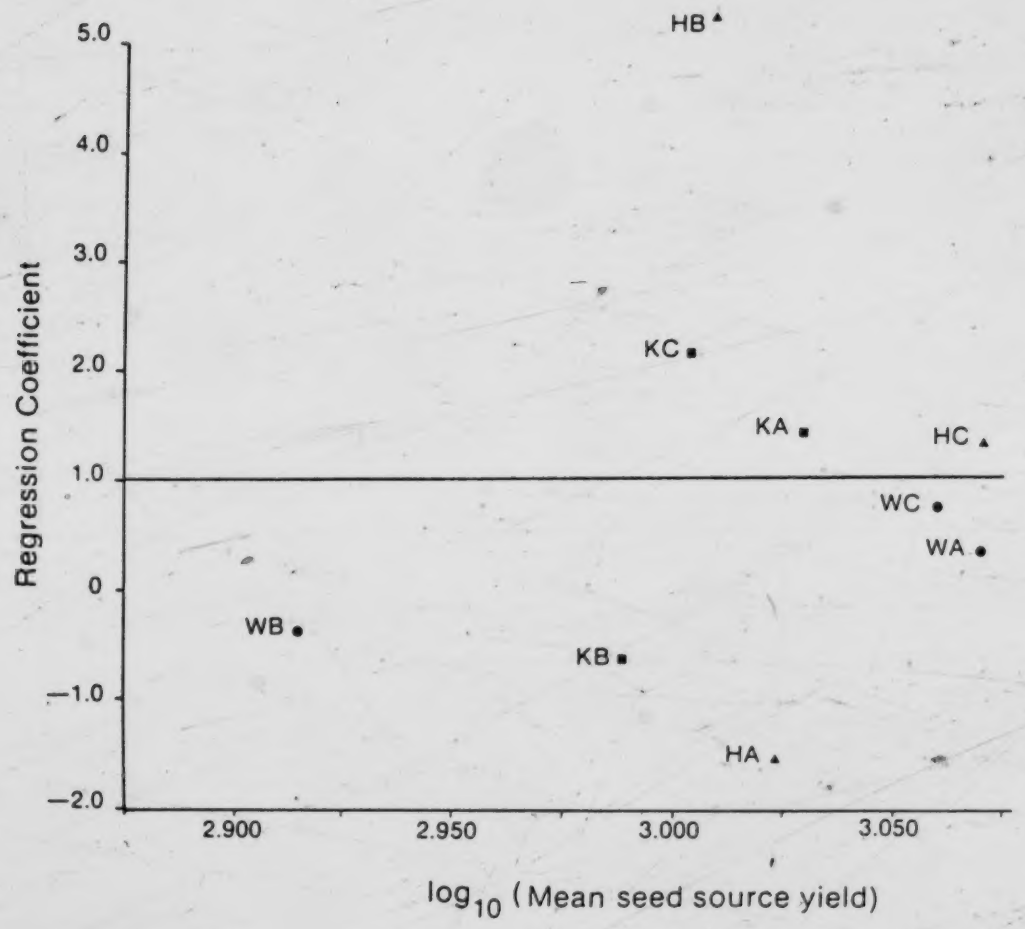
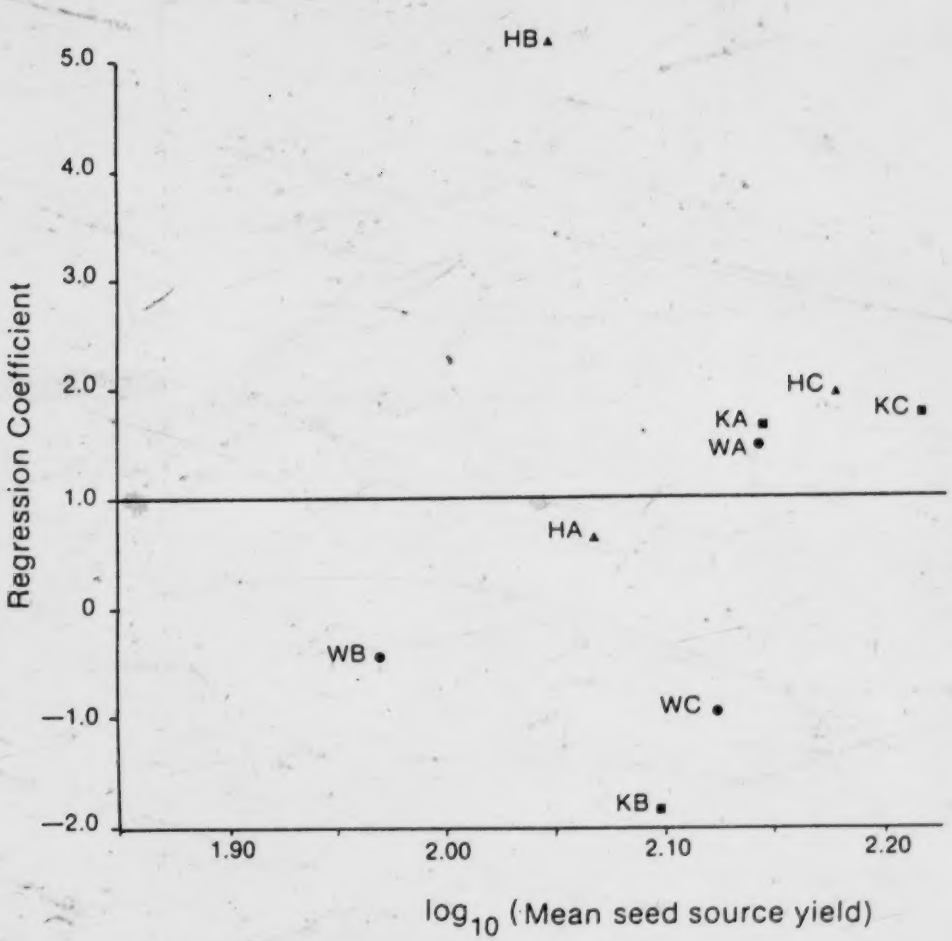


Figure IV.21. Scatter diagram; root dry weight data for the hydroponic progeny test. Regression coefficient (b) derived from the equation

log(site mean) = a + b · log(treatment mean) is plotted against log(site mean).



above-ground dry weight data (Figure IV.22) the reverse was true. Similarly, KC root production was most tolerant or adapted to both conditions whereas for total and above-ground dry weight production, the WC, HC and WA sites held this position.

Finally, for leaf dry weight, Figure IV.23 shows the pattern is one of high general adaptability of HC, WA and WC seed source sites; specific adaptability to non-Al conditions for HB, KA, KC sites; specific positive response of HA and KB sites to aluminum and a neutral, poor response for WB.

Figure IV.22. Scatter diagram; above-ground dry weight for the hydroponic progeny test.
regression coefficient (b) derived from the equation
log(site mean) = a + b · log(treatment mean) is plotted against log(site mean).

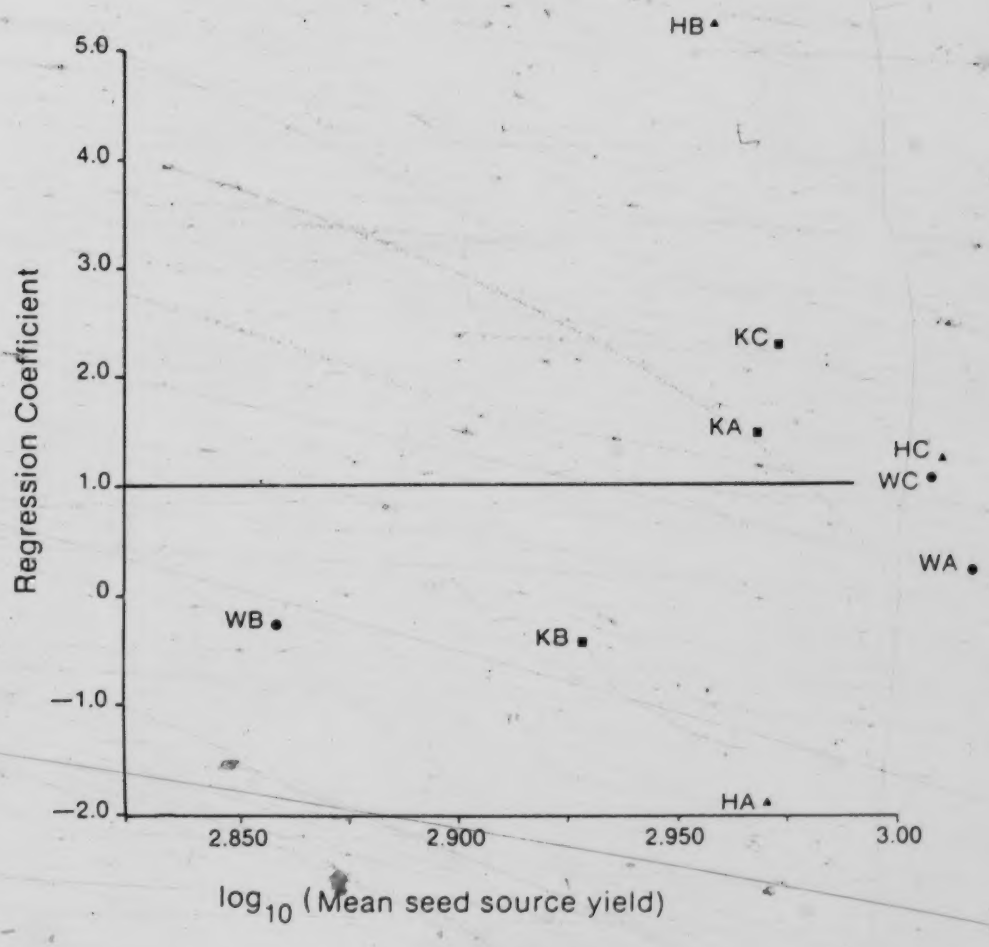
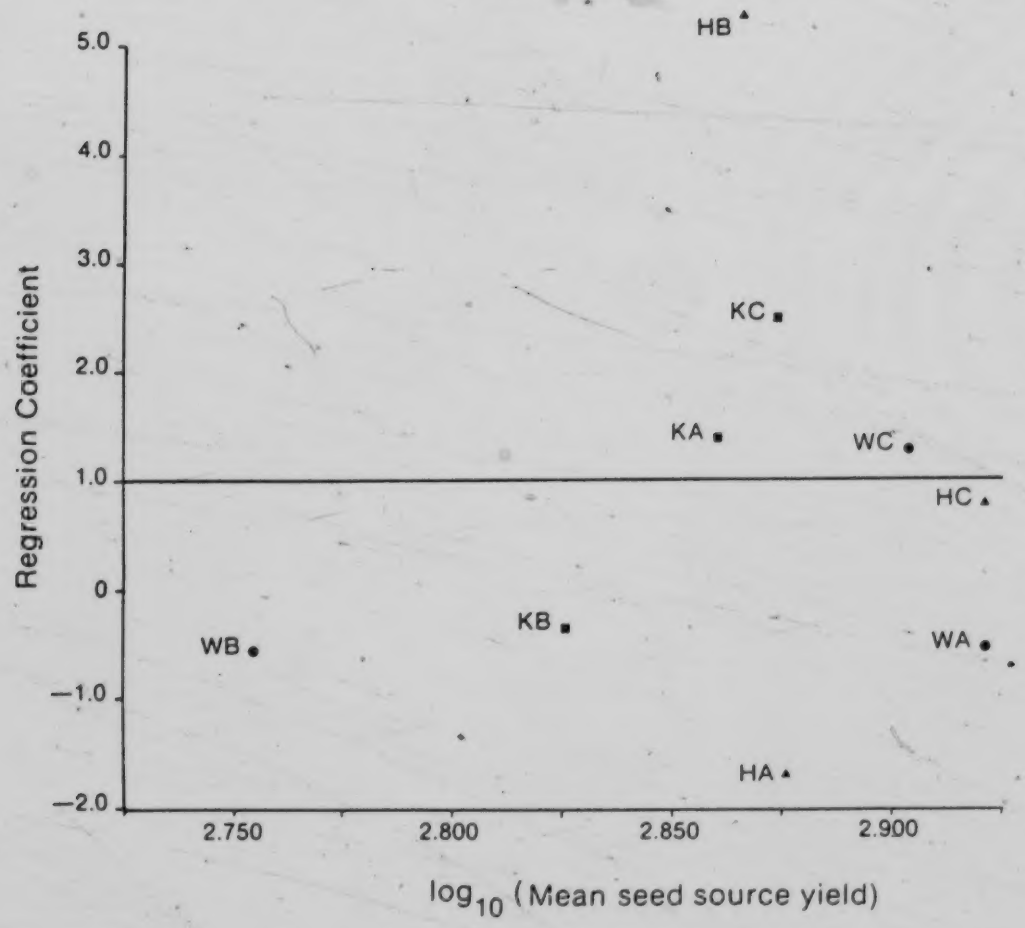


Figure IV.23. Scatter diagram; leaf dry weight data for the hydroponic progeny test. Regression coefficient (b) derived from the equation

$$\log(\text{site mean}) = a + b \cdot \log(\text{treatment mean})$$

is plotted against log(site mean).



V. CONCLUSIONS

In part, the objective of this project was to determine whether Alberta's white spruce populations comprised individuals harboring wide physiologic plasticity, or rather separate sub-populations each specifically adapted to a narrow range of soil conditions. With seeds of numerous origin grown in different rooting environments and with growth parameters monitored for estimates of performance, the soil composite progeny test tended to support the fact that neither extreme has been reached in the evolutionary development of the species; populations differed markedly in the degree of specialization towards parental rooting habitat. By growing well on the acidic soil composite while also incurring the least growth inhibition on the calcareous treatment, the Hinton provenance exhibited broader adaptability than Whitecourt or Keg River seed sources.

In the regression coefficient scatter diagrams (Figures IV.15 to IV.23), simple linear regression was used to reveal the intra-region variation that may reflect adaptability patterns. They serve to describe various types of varietal adaptations to a range of environments and are used as a quantitative measure of phenotypic plasticity.

For each region, one of the three sampled sites had treatment means placing it in an area of high general adaptability, according to the evaluation format developed by Finlay and Wilkinson (1962). For HA, WA and KC sites, seedling performance in terms of total and root dry weight was consistently high and insensitive to the range of chemical and biological conditions imposed by the natural soil substrates. More than either of the other two Whitecourt sites, seedlings of the WA site tended to occur further than the other two above a regression coefficient of 1.0, hence possessed above average stability. High relative performance of seedlings from these three areas on the favorable Whitecourt and Keg River substrates may be of utility to tree breeders. For successful reforestation programs, such 'ideal' varieties may be sought, whereby outplanted stock would have maximum yield in the most favorable soil environments and maximum phenotypic stability in all environments.

KA was marked by above-average stability. Although it exhibits little change in yield despite large changes in the environment, its mean yield on all substrates is consistently below average. Owing to genetic inferiority, its many sampled families may be poor candidates for nursery selection and breeding schemes. The final Keg River site, KB, should be regarded likewise, as poorer-than-average growth marks the seed stock as less than desirable.

Perhaps not unexpectedly, HB and HC populations grew well on the unfavorable environments, which in this case is the Hinton soil. These seed source sites produced seedlings with superior growth and hence, may be considered for reforestation of such calcareous lands.

The implications of such morphological assessments is possible because of the conceptual models developed to explain genetic variations in growth. Ledig (1974) stated that total plant dry weight is a simple multiple of the weight of organic carbon metabolically assimilated as CO_2. Growth differences are, in part, due to differences in CO_2 uptake. In a study of 26 *Pinus taeda* families, Ledig observed that 64% of the variation in plant total dry weight could be explained by net assimilation rate differences (net CO_2 uptake minus CO_2 loss by respiration, multiplied by a constant which is a ratio of dry weight increments per gram of CO_2 assimilated). Thus, photosynthetic capabilities in response to a physical, biological or chemical factor are used to determine ranges of provenance adaptation and suitability to particular environmental regimes. The morphological and anatomical traits assessed here may be of equal utility for early progeny evaluation and provenance selection.

Extending the concept, one may assume that inorganic nutrient fluxes and organic assimilate distribution patterns exist within a plant. Variations in these patterns constitute the genetic variation observed in seedling growth among provenances and along environmental gradients. The strength of genetically inherent models of dry matter partitioning may be discerned in Figures IV.13 and IV.14. On the acidic soil substrate (Figure IV.13), the Keg River seed source region allocates a greater proportion of assimilated carbon into root biomass. The lowest region for root production is Hinton, the alkaline-origin provenance. On average, Hinton seedlings accumulated the greatest amount of dry weight into leaves. Thus, on the most

productive treatment, the acidic and alkaline sub-populations distinguished themselves on the basis of dry matter partitioning.

The assessments made from the progeny tests reveal how the three seed sources differ in adaptive strategies and performance potential. From the soil composite progeny test, the Hinton seed source region incurred the lowest mortality rates before harvesting, along with the highest total dry weight average. This would seem to suggest that the provenance is broadly adapted to the three soil regimes presented. In the presence of natural soil biological influences, including mycorrhizae, the Hinton seedlings collectively exhibited stongest vigor, even on a foreign soil regime, such as the Keg River composite. In terms of root dry weight, Keg River seedlings had the highest level of growth on the Keg River soil, whereas Hinton seedlings had the highest on their parental soil. Although the interaction is statistically insignificant, this trend may indicate the high selectivity of Keg River roots to acidic soils. The seed source ranks lowest on the Hinton soil, hence is more narrowly adapted than Hinton seed.

Hinton seedlings did not have high relative root growth on Keg River soil, but they did maintain high leaf production. Hinton seedlings inherently emphasized leaf production to a degree exceeding that observed in Whitecourt and Keg River populations. This fact is exhibited in the consistently high shoot:root ratios of the Hinton progeny, compared to Keg River seedlings.

For all seed source regions, growth is maximal on Keg River soil. Therefore, white spruce may be genetically well-adapted to acidic conditions, given the influence of soil microorganisms. Mycorrhizae, as partial mediators of root physiologic activities, may shelter plant roots from those metals, particularly aluminum, which are increasingly soluble at low pH.

Keg River seedlings may be narrowly adapted to the species of mycorrhizal fungi predominating at low pH, whereas Hinton seedlings may be generally more receptive to a wider range of fungi including those residing in the calcareous substrate. Although frequency of mycorrhizal tips is approximately equal among seed sources and among soils (Table IV.7), it may be possible that Hinton and Keg River seedlings differed in metabolic capabilities,

subsequent to fungal colonization. Varying abilities of fungi, as part of the host:microbe complex, to sequester soil cations either to protect roots from metal toxicity may explain the breadth of seed source region adaptations. The possession of physiologic Al tolerance or avoidance mechanisms may also be the basis upon which the provenances may differ.

Sampling of 3 sites per region may not have provided sufficient replication. The considerable variability among sites within regions, as illustrated in the soil chemical analyses of Appendix C, may have contributed to the variability expressed in the seed source site averages.

In the hydroponics experiment, the Hinton seedling dominance in non-Al solution was lost on the aluminum solution. Therefore, the competitive advantage of the seedlings in acidic conditions may be dependent on soil biological factors. On the Al treatment, the Keg River seedlings outperformed those of Hinton and therefore, may have root adaptations for the ability to fulfill normal physiologic functions in the presence of free forms of aluminum.

With respect to the soil composite progeny test, the findings applying to the original null hypotheses may be summarized as follows:

1. Soil type affects white spruce performance and survival. White spruce is adapted to acidic conditions, given the presence of natural soil biotic features. Calcareous substrates represent the poorest productivity potential for the species.

2. White spruce seedlings of differing origin may possess a unique response to differing soil types. Calcareous-originating seed is most broadly adapted to the substrates tested, whereas acid-originating provenances appear most responsive to acidic conditions.

3. There was no evidence of genotype X environment interactions. Not all seed sources, ranked on the basis of phenotypic expression, were superior on their parental soil composites. Similarly, not all provenances were inferior on non-parental soils. The Hinton provenance was consistently superior on all treatments.

With respect to the null hypotheses of the hydroponic progeny test the following points may be made:

4. The acid-originating seedlings are relatively insensitive to Al in solution culture and hence,

may possess roots systems with physiological mechanisms specifically adapted to the presence of free forms of Al, even in the absence of mycorrhizae.

5. Comparisons of relative seed source productivity between the soil composite and hydroponic progeny tests indicate that the capability of the calcareous-originating population to outperform others in rooting conditions where free ionic forms of aluminum may exist is dependent upon the presence of biological interactions, as part of the rhizosphere. In sterile solution cultures, the calcareous provenance is most highly inhibited if Al is present.

6. Hinton seedlings possess a greater inherent emphasis on leaf production than Keg River seed. This trend persists in all natural soil substrates.

7. There is marked variablity in site performance within regions. Therefore, any tree improvement program, involving an initial search for desirable material, should also involve a test of as many families as possible from the regions whose response to specific soil properties is of interest.

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APPENDIX A

Soil Profile and Plant Community from Sampled Stands

Table A1. Soil Profile Descriptions; Hinton site 'A'
Orthic Melanic Brunisol, Kia Nea series.

Horizon	Depth (cm)	Description
		Pit no.1
L	2-0	
Ahk	0-28	black(7.5YR 2/1 m), dark brown(10YR 3/3 d); loam; fine single grain; very friable; plentiful fine oblique and abundant medium to coarse horizontal roots; clear wavy boundary.
Bmk_1	28-46	reddish brown (5YR 4/6 m), bright brown(7.5YR 5/6 d); sandy loam; fine single grain; very friable; plentiful fine oblique and plentiful medium horizontal roots; gradual smooth boundary.
Bmk_2	47-68	brown(10YR 4/6 m), bright yellowish brown(10YR 6/8 d); sandy loam; fine single grain; very friable; few fine and medium vertical roots; diffuse smooth boundary.
Ck	87-125	dull yellowish brown(10YR 5/4 m), dull yellow orange(10YR 6/3 d); sand; single grain; loose; very few very fine oblique roots. cobble layer begins at 125 cm. gravelly layer at 68 cm. 19-23 cm thick. Coarse fragments from pebble to cobble size.
		Pit no. 2
L	2-0	
Ahk	0-27	brownish black(7.5YR 2/2 m), dark brown (10YR 3/3 d); loam; fine single grain; very friable; abundant fine to medium oblique and coarse horizontal roots; gradual smooth boundary.
Bmk_1	27-45	brown(7.5YR 4/6 m), yellowish brown(10YR 5/6 d); sandy loam; fine single grain; very friable; plentiful fine to medium oblique roots; clear smooth boundary.
Bmk_2	45-59	yellowish brown(10YR 5/6 m), bright yellowish brown(10YR 6/6 d); sandy loam; fine single grain; very friable; plentiful very fine to fine vertical roots; gradual smooth boundary.
IICk	59-110	olive brown(2.5Y 4/4 m), dull yellow (2.5Y 6/4 d); clay loam; weak to moderate platy; firm; very few fine exped roots. cobbly rock fragments at 59 cm, discontinous, 0-9 cm thick. coarse fragments content by volume <5%.

Table A2. Soil Profile Descriptions; Hinton site 'B'
Cumulic Regosol, Orge series.

Horizon	Depth (cm)	Description
		Pit no.1
L	1-0	
Ahjk	0-29	brownish black(10YR 3/2 m), grayish yellow brown(10YR 4/2 d); loamy sand; fine single grain; very friable; abundant fine oblique roots; diffuse wavy boundary.
Ck	29-135	dark brown(10YR 3/3 m), dull yellow brown (10YR 5/3 d); loamy sand; fine single grain; very few fine vertical roots.
		Pit no.2
L	1-0	
Ahjk	0-27	brownish black(10YR 3/2 m), dull yellow brown (10YR 5/3 d); sandy loam; fine single grain; abundant fine to medium horizontal roots; diffuse wavy boundary.
Ck	27-130	dark brown(10YR 3/3 m), dull yellowish brown(10YR 5/3 d); loamy sand; fine single grain; very friable; few fine oblique roots.

Table A3. Soil Profile Descriptions; Hinton site 'C'
Orthic Melanic Brunisol, Kia Nea series.

Horizon	Depth (cm)	Description
		Pit no.1
L	8-6	
F	6-0	
Ahk	0-12	brownish black(5YR 2/2 m), (5YR 3/2 d); silty loam; very weak very fine platy; very friable; plentiful fine and medium horizontal roots; gradual wavy boundary.
Bmk_1	12-16	dark reddish brown(5YR 3/4 m), dull brown(7.5YR 5/3 d); silty loam; very weak, very fine platy; very friable; plentiful fine oblique roots; clear wavy boundary.
$Ahbk_1$	17-30	dark brown(10YR 3/3 m), dull yellowish brown(10YR 5/3 d); silty loam; very weak very fine platy; very friable; plentiful fine oblique roots; gradual wavy boundary.
$Ahbk_2$	30-53	dull yellowish brown(10YR 4/3 d), silty loam; very weak medium subangular blocky; very friable; plentiful fine oblique roots;gradual wavy boundary.
Bmk_2	53-60	dark reddish brown(5YR 3/2 m), brown (7.5YR 4/4 d); silty loam; very weak fine platy; loose; plentiful fine oblique roots;clear wavy boundary.
Bmk_3	60-79	dark reddish brown(5YR 3/2 m), brown (7.5YR 4/4 d); silty loam; very weak fine subangular blocky; very friable; few fine oblique roots; clear smooth boundary.
BCk	79-100	dull reddish brown(5YR 3/2 m); silty loam; very weak fine subangular blocky to massive; very friable; few fine oblique roots; clear smooth boundary.
Ck	100-120	reddish brown(5YR 3/2 m), bright brown (7.5YR 5/6 d); silty loam; massive; very friable; very few fine oblique roots.
		Pit no.2
L	6-3	
F	3-0	
Ahk	0-12	brownish black(10YR 2/2 m), brownish black(10YR 3/2 d); silty loam; single grain; loose; abundant very fine and fine oblique roots; gradual smooth boundary.
$Ahbk_1$	12-27	brownish black(7.5YR 3/2 m), grayish yellow brown(10YR 5/2 d); silty loam; very weak fine platy; friable; plentiful fine and medium exped oblique roots; clear smooth boundary.
$Ahbk_2$	27-44	brownish black(7.5YR 3/2 m), grayish yellow brown(10YR 4/2 d); loam; weak fine platy; friable; plentiful fine and medium exped oblique roots; clear smooth boundary.
Bmk_1	44-51	dull reddish brown(5YR 3/2 m), dull brown(7.5YR 5/4 d); loam;very weak fine platy; friable; plentiful fine and medium vertical exped roots; clear smooth boundary.
Bmk_2	51-86	dark reddish brown(5YR 3/2 m), brown(7.5YR 4/3 d); loam; very weak fine platy; very friable; plentiful fine and medium exped roots; clear smooth boundary.
Ck_1	86-100	bright reddish brown(5YR 5/6 m), orange(7.5YR 6/6 d); sandy loam; massive; few fine vertical roots; clear smooth boundary.

Ck_2	110-125	dull yellowish brown(10YR 4/3 m), dull yellow orange (10YR 6/3 d); sandy loam; massive; firm; very few very fine roots.

Table A4. Soil profile descriptions; Whitecourt site 'A'
Orthic Gray Luvisol, Hubalta series.

Horizon	Depth (cm)	Description
		Pit no.1
L	8-6	
F	6-0	abundant medium and coarse horizontal roots; abrupt wavy boundary.
Ae_1	0-8	dark brown(10YR 3/3 m), brownish gray(10YR 6/1 d); sandy loam; very weak fine platy; very friable; plentiful medium and coarse horizontal exped roots; clear wavy boundary.
Ae_2	8-25	dull yellowish brown(10YR 5/3 m), light gray(10YR 7/1 d);sandy loam; very weak fine platy; very friable; few fine to fine oblique inped roots; clear smooth boundary.
AB	25-38	dull yellowish brown(10YR 5/3 m), light gray(10YR 7/1 d); loam; weak fine subangular blocky; friable; few fine to very fine oblique inped roots; clear smooth boundary.
Bt_1	38-55	brown(10YR 4/4 m), grayish yellow brown(10 YR 6/2 d); clay loam; weak fine subangular blocky; friable; very few fine oblique inped roots; gradual smooth boundary.
Bt_2	55-80	dull yellowish brown(10YR 4/3 m), grayish yellow brown(10YR 6/2 d); clay loam; moderate medium subangular blocky; friable; very few very fine oblique inped roots; gradual smooth boundary.
BC	80-110	dull yellowish brown(10YR 5/3 m), dull yellow(2.5Y 6/3 d); clay loam; weak medium prismatic to weak medium subangular blocky; friable; very few very fine vertical inped roots; gradual smooth boundary.
C	110-125	dull yellowish brown(10YR 5/3 m), yellowish brown(10YR 5/3 d); clay loam; massive; firm; gradual smooth boundary.
		moderately well to well drained.
		coarse fragments <10% by volume.
		Pit no.2
L	8-6	
F	6-0	abundant medium horizontal and plentiful fine horizontal roots; abrupt wavy boundary.
Ae_1	0-7	grayish yellow brown(10YR 6/2 m), brownish gray(10YR 6/1 d); sandy loam; very weak fine platy; very friable; plentiful fine horizontal inped roots; clear wavy boundary.
Ae_2	7-21	dull yellowish brown(10YR 5/3 m), grayish yellow brown(10YR 6/2 d); sandy loam; very weak fine platy; very friable; few fine oblique inped roots; clear wavy boundary.
AB	21-31	dull yellowish brown(10YR 5/3 m), dull yellow orange(10YR 7/3 d); loam; weak fine subangular blocky; very friable; few fine oblique inped roots; gradual wavy boundary.
Bt_1	31-54	brown(10YR 4/4 m), dull yellow orange(10YR 6/4 d); clay loam; weak fine to medium subangular blocky; friable; very few fine oblique inped roots; gradual smooth boundary.

Bt_2	54-73	dull yellow orange(10YR 6/4 d); clay loam; weak medium blocky; friable; very few fine oblique inped roots; gradual smooth boundary.
BC	73-90	dull yellow(2.5Y 6/4 d); clay loam; weak medium blocky; friable; very few very fine inped and exped roots; gradual smooth boundary.
C_1	90-97	yellowish brown(2.5Y 5/4 d); clay loam; massive; coarse fragments <2% by volume, cobble-sized.

Table A5. Soil profile descriptions; Whitecourt site 'B'
Orthic Gray Luvisol, Hubalta series.

Horizon	Depth (cm)	Description
		Pit no.1
L	8-5	
F	5-0	abundant coarse and medium horizontal roots; abrupt smooth boundary.
Ae_1	0-3	dark brown(10YR 3/3 m); loam; weak fine platy; friable; plentiful fine horizontal inped roots; abrupt wavy boundary.
Ae_2	3-16	dull yellowish brown(10YR 5/3 m), light gray(10YR 8/2 d); loam; weak fine platy; friable; plentiful fine horizontal inped roots; clear wavy boundary; 10 to 26 cm thick.
AB	16-21	dull yellowish brown(10YR 5/4 m), dull yellow orange(10YR 6/4 d); clay loam; weak fine subangular blocky; friable; plentiful medium horizontal inped roots; clear smooth boundary; 3 to 5 cm thick.
Bt_1	21-32	dull yellowish brown(10Yr 4/3 m, 10YR 5/3 d); clay loam; weak medium prismatic to weak subangular blocky; firm; few fine oblique inped roots; abrupt smooth boundary.
$IIBC_1$	32-55	brown(10YR 4/4 m), yellowish brown(2.5Y 5/6 d); sandy loam; very weak medium subangular blocky to massive; firm; very fine oblique inped roots; abrupt smooth boundary;
$IIBC_2$	55-80	dull yellowish brown(10YR 5/4 m), yellowish brown(10YR 5/6 d); sandy loam; horizontal streaks of dark reddish brown(2.5 YR 3/6 m) mottles; massive; firm; very few fine vertical inped roots; clear smooth boundary.
$IIBCk_3$	80-115	yellowish brown(10YR 5/6 m), olive brown(2.5Y 4/6 d); sandy loam; massive; very friable; few fine oblique roots; clear smooth boundary.
IICk	115-130	yellowish brown(10YR 5/4 m), grayish yellow brown(10YR 6/2 d); massive; loose.
		Pit no.2
L	8-6	
F	6-0	abundant medium and coarse horizontal roots; abrupt wavy boundary.
Ae	0-29	dull yellowish brown(10YR 5/3 m), light gray(10YR 7/1 d); loam; very weak fine platy; very friable; plentiful very fine to fine oblique inped roots; clear wavy boundary.
AB	29-33	dull yellowish brown(10YR 5/3 m), brownish gray(10YR 6/1 d); clay loam; weak fine platy; friable; plentiful very fine to fine oblique imped roots; clear wavy boundary;
Bt	33-61	dull yellowish brown(10YR 4/3 m), grayish yellow brown(10YR 6/2 d); clay loam; moderate fine subangular blocky; friable; few fine vertical inped roots; clear smooth boundary.
BC	61-84	dull yellowish brown(10YR 4/3 m), grayish yellow brown(10YR 6/2 d); clay-clay loam; weak medium prismatic to weak medium blocky; firm; few very fine vertical exped roots; gradual smooth boundary.

Ck_1	84-112	dull yellowish brown(10YR 4/3 m), grayish yellow brown(10YR 6/2 d); clay-clay loam; massive; firm; few very fine vertical roots; gradual smooth boundary.
Ck_2	112-120	moderately-well to well drained coarse fragments <2% cobbles.

Table A6. Soil profile descriptions; Whitecourt site 'C'
Orthic Gray Luvisol, Hubalta series.

Horizon	Depth (cm)	Description
		Pit no.1
L	9-7	
F	7-0	many medium to coarse horizontal roots; abrupt smooth boundary.
Ae	0-12	grayish yellow brown(10YR 5/2 m), light gray(10 7/1 d); sandy loam; weak fine platy; very friable; plentiful very fine to fine oblique exped roots; clear smooth boundary.
AB	12-20	dull yellowish brown(10YR 4/3 m), dull yellow orange(10YR 6/3 d); sandy loam; weak fine subangular blocky; friable; plentiful very fine to fine oblique exped roots; clear smooth boundary.
Bt_1	20-40	dull yellowish brown(10YR 5/3 m), dull yellow orange (10YR 6/3 d); loam; moderate to strong fine subangular blocky; firm; plentiful very fine to fine oblique exped roots; gradual smooth boundary.
Bt_2	40-68	dull yellowish brown(10YR 5/3 m), yellowish brown(2.5 Y 5/3 d); loam; moderate medium subangular blocky; firm; plentiful very fine to medium oblique inped roots; gradual smooth boundary.
BC	68-90	dull yellowish brown(10YR 4/3 m), yellowish brown(2.5Y 5/3 d); clay loam; weak medium prismatic to moderate medium blocky; firm; very few very fine vertical exped roots; gradual smooth boundary.
Ck_1	90-100	dull yellowish brown(10YR 4/3 m), olive brown(2.5 Y 4/3 d); clay loam; massive; very few very fine vertical roots; gradual smooth boundary.
Ck_2	100-115	moderately well drained. coarse fragments <2% cobbles.
		Pit no.2
L	9-7	
F	7-0	many medium to coarse horizontal roots; abrupt smooth boundary.
Ae_1	0-13	dull yellowish brown(10YR 4/3 m), grayish yellow brown (10YR 6/2 d); loam; weak fine platy; very friable; plentiful very fine and fine oblique exped roots; clear wavy boundary.
Ae_2	13-19	dull yellowish brown(10YR 5/3 m), light gray(10YR 7/1 d); loam; weak fine platy; very friable; plentiful fine and medium oblique exped roots; clear smooth boundary.
Bt_1	19-34	dull yellowish brown(10YR 4/3 m); clay; moderate fine subangular blocky; firm; plentiful fine oblique inped roots; clear smooth boundary.
Bt_2	34-56	dull yellowish brown(10YR 4/3 m), yellowish brown(2.5Y 5/3 d); clay; moderate medium blocky; firm; few fine oblique inped roots; clear smooth boundary.

BC	56-76	dull yellowish brown(10YR 4/3 m), yellowish brown(2.5Y 5.3 d); clay loam; weak to moderate medium prismatic to moderate medium blocky; firm; very few fine vertical exped roots; clear smooth boundary.
Ck_1	76-95	dark brown;(10YR 3/3 m); clay loam; massive; firm; smooth boundary.
Ck_2	95-110	dark brown(10YR 3/3 m), yellowish brown(2.5Y 5/4 d); clay loam; massive.

well drained.
coarse fragments <2% cobbles.

Table A7. Soil profile Descriptions; Keg River site 'A'
Boundary series.

Horizon	Depth (cm)	Description
		Pit no.1
L	7-5	
F	5-0	
Ae	0-13	grayish yellow brown(10YR 6/2 m); loam; friable; moderate fine platy; plentiful fine and medium horizontal roots; abrupt wavy boundary.
AB	13-21	bright yellowish brown(10YR 6/6 m); clay loam; weak fine subangular blocky; friable; plentiful medium oblique exped roots; clear wavy boundary.
Bt_1	21-35	dull yellowish brown(10YR 5/4 m), clay loam; moderate fine to medium subangular blocky; friable; plentiful fine, few medium oblique exped roots; clear smooth boundary.
Bt_2	35-53	dull yellowish brown(10YR 4/3 m); clay; moderate medium prismatic to weak medium blocky: firm; plentiful very fine oblique inped and exped roots; clear smooth boundary.
IIBC	53-100	dull yellowish brown(10YR 5/4 m); sandy loam; weak medium blocky to massive; clear smooth boundary.
IIC	100-110	olive brown(2.5Y 4/4 m); sandy loam; massive; common fine prominent mottles. cobble and pebble sized fragments at 73 cm, 5 to 8 cm thick. coarse fragments up to 50% by volume in BC horizon.
		Pit no.2
L	8-4	
F	4-0	
Ae	0-13	grayish yellow brown(10YR 6/2 m); loam; weak fine platy; very friable; plentiful fine and medium exped roots; abrupt wavy boundary.
AB	13-29	yellowish brown(10YR 5/6 m); clay loam; very weak fine platy; very friable; plentiful fine and medium exped roots; clear wavy boundary
Bt_1	29-43	dull yellowish brown(10YR 4/3 m); clay loam; moderate fine to medium subangular blocky; friable; few fine inped and exped roots; gradual smooth boundary.
Bt_2	43-65	gray(7.5Y 5/1 m); moderate to strong medium subangular blocky; firm; very few fine exped roots; gradual smooth boundary.
Bt_3	65-90	gray(7.5Y 5/1 m); clay; few fine prominent mottles; moderate fine to medium subangular blocky; firm; diffuse smooth boundary.
Bt_4	90-110	gray(7.5Y 5/1 m); clay; common fine prominent mottles; moderate medium subangular blocky; very firm.

Table A8. Soil profile descriptions; Keg River site 'B'
Boundary series.

Horizon	Depth (cm)	Description
		Pit no.1
L	8-5	
F	5-0	
Ah	0-15	brownish black(10YR 2/2 m); clay loam; fine granular; very friable; plentiful fine oblique and medium horizontal exped roots; abrupt wavy boundary.
Bt_1	15-34	dull yellowish brown(10YR 4/3 m); clay; moderate medium subangular blocky; friable; plentiful fine and medium oblique inped and exped roots; clear smooth boundary.
Bt_2	34-52	grayish yellow brown(10YR 5/2 m); clay; moderate medium subangular blocky; friable; plentiful fine to medium oblique inped and exped roots; gradual smooth boundary.
Bt_3	52-100	grayish yellow brown(10YR 4/2 m); clay; moderate fine to medium subangular blocky; firm; few fine vertical inped and exped roots; gradual smooth boundary.
BC	100-110	brown(10YR 4/4m); clay moderate medium subangular blocky to massive; firm; very few very fine vertical exped roots.
C	110-120	brown(10YR 4/4 m); clay; common fine distinct mottles; massive; firm; very few very fine vertical roots.
		Pit no.2
L	7-5	
F	5-0	
Ahe	0-12	brownish black(10YR 2/2 m); loam; weak fine platy to granular; loose; abundant fine to medium horizontal roots; plentiful fine to medium oblique roots; clear wavy boundary.
AB	12-30	dull yellowish brown(10YR 5/4 m); clay loam; moderate fine to medium platy; very friable; plentiful fine and medium oblique inped roots; gradual smooth boundary.
Bt_1	30-50	brown(10YR 4/4m); clay; weak to moderate medium blocky; firm; few fine to medium vertical roots; gradual smooth boundary.
Bt_2	50-90	brown(10YR 4/4 m); clay; weak fine blocky; firm; very few very fine vertical exped roots; diffuse smooth boundary.
Bt_3	90-100	brown(10YR 4/4 m); clay; moderate medium blocky to massive; firm; very few very fine vertical exped roots.
C	100-110	brown(10YR 4/4m); clay; massive; firm; very few very fine vertical roots.
		coarse fragments <1% cobbles.

Table A9. Soil profile descriptions; Keg River site 'C'
Boundary series.

Horizon	Depth (cm)	Description
		Pit no.1
L	7-2	
F	2-0	
Ah	0-15	brownish black(10YR 3/2 m); clay loam; single grain; very friable; plentiful fine oblique and medium horizontal roots; abrupt wavy boundary.
Bt_1	15-34	dull yellowish brown(10YR 4/3 m); clay; moderate medium subangular blocky; friable; plentiful fine and medium oblique inped and exped roots; clear smooth boundary.
Bt_2	34-52	grayish yellow brown(10YR 5/2 m); clay; moderate medium subangular blocky; firm; plentiful fine to medium oblique exped roots; gradual smooth boundary.
BC	52-95	grayish yellow brown(10YR 4/2 m); clay; very fine subangular blocky; firm; few fine vertical inped and exped roots; gradual smooth boundary.
C	95-110	brown(10YR 4/4 m); clay; common fine distinct mottles; moderate very fine subangular blocky to weak medium prismatic; firm; very few very fine vertical exped roots.
		Pit no.2
L	7-3	
F	3-0	
Ah	0-7	brownish black(10YR 3/2 m); clay loam; single grain; very friable; plentiful fine oblique and plentiful medium horizontal roots; clear irregular boundary.
Bt_1	7-38	dull yellowish brown(10YR 5/4 m); clay loam; friable; medium to strong coarse subangular blocky; plentiful fine oblique and plentiful medium horizontal inped and exped roots; gradual wavy boundary.
Bt_2	38-100	brown(10YR 4/4 m); clay; strong medium blocky; few fine vertical exped roots; diffuse wavy boundary.
C	100-110	dull yellowish brown(10YR 5/4 m); clay; common medium faint mottles; massive; firm; very few fine vertical roots.

APPENDIX B

Plant Community Descriptions

Table B.1. Plant Community Descriptions; Hinton Region.

Trees	Shrubs	Herbs & Grasses	Mosses
		Site 'A'	
10-30% cover	10-20%	80-90%	10-20%
Picea glauca	*Cornus stolonifera* *Juniperus horizontalis* *Lonicera dioica* *Rosa acicularis*	*Aquilegia flavescens* *Arctostaphylos uva-ursi* *Galium borealis* *Habenaria viridis* *Linnaea borealis* *Primula incana* *Pyrola secunda* *Stellaria longifolia* *Vicia americana* *Viola orbiculata* *Lathyrus ochroleucus*	*Dicranum polysetum* *Distichium capillaceum* *Ptilium crista-castrensis*
		Site 'B'	
40-50% cover	10-20%	50-60%	0-10%
Picea glauca	*Juniperus communis* *Populus tremuloides* *Rosa acicularis* *Sheperdia canadensis* *Symphoricarpos albus* *Viburnum edule*	*Anenome parviflora* *Calypso bulbosa* *Cornus canadensis* *Equisetum sp.* *Erigeron grandiflorus* *Linnaea borealis* *Orchis rotundifolia* *Pyrola secunda* *Stellaria longifolia* *Stenanthium occidentale* *Viola orbiculata* *Viola rugulosa*	*Ptilium crista-castrensis*

Table B1. Plant Community Desriptions; Hinton Region (cont'd).

Site 'C'			
40-50 cover	0-10%	80-90%	40-50%
Picea glauca	*Juniperus communis* *Populus tremuloides* *Prunus virginiana* *Rosa acicularis* *Sheperdia canadensis* *Symphoricarpos albus* *Viburnum edule*	*Arctostaphylos uva-ursi* *Calypso bulbosa* *Cornus canadensis* *Equisetum sp.* *Linnaea borealis* *Orchis rotundifolia* *Pyrola secunda* *Stellaria longifolia* *Viola orbiculata* *Viola rugulosa*	*Ptilium crista-castrensis*

Table B2. Plant Community Descriptions; Whitecourt Region.

Trees	Shrubs	Herbs & Grasses	Mosses
		Site 'A'	
20-30% cover	60-70%	20-30%	10-20%
Abies balsamea *Picea glauca (20%)* *Populus balsamifera*	*Amelanchier alnifolia* *Lonicera involucrata* *Ribes sp.* *Rosa acicularis* *Rubus strigosus* *Symphoricarpos albus* *Viburnum sp.*	*Aralia nudicaulis* *Arnica cordifolia* *Aster sp.* *Clematis sp.* *Cornus canadensis* *Epilobium sp.* *Galium boreale* *Gymnocarpium dryopteris* *Linnaea borealis* *Mertensia paniculata* *Pyrola asarifolia* *Smilacina racemosa* *Viola renifolia*	*Hylocomium splendens* *Lycopodium annotinum* *Pleurozium schreberi* *Ptilium crista-castrensis*
		Site 'B'	
30-40 cover	30%	20%	50%
Picea glauca (40%) *Populus tremuloides*	*Lonicera involucrata* *Ribes sp.* *Rubus strigosus* *Vibernum edule*	*Anenome parviflora* *Aralia nudicaulis* *Arnica cordifolia* *Cornus canadensis* *Epilobium sp.* *Hieracium canadense* *Lathyrus ochroleucus* *Linnaea borealis* *Mertensia paniculata* *Mitella nuda* *Petasites sp.* *Pyrola asarifolia*	*Hylocomium splendens* *Lycopodium annotinum* *Pleurozium schreberi* *Ptilium crista-castrensis*

Table B2. Plant Community Descriptions; Whitecourt Region (cont'd).

Site 'C'			
40-50 cover	<10%	30-40%	30-40%
Abies balsamea	*Fragaria virginiana*	*Achillea sibrica*	*Hylocomium splendens*
Betula papyrifera	*Lonicera involucrata*	*Cornus canadensis*	*Lycopodium annotinum*
Picea glauca (40%)	*Ribes sp.*	*Linnaea borealis*	*Pleurozium schreberi*
Populus balsamifera	*Viburnum edule*	*Malanthemum canadense*	*Ptilium crista-castrensis*
Populus tremuloides		*Mitella nuda*	
		Petasites sp.	
		Pyrola asarifolia	
		Pyrola secunda	
		Viola renifolia	

Table B3. Plant Community Descriptions; Keg River Region.

Trees	Shrubs	Herbs & Grasses	Mosses
		Site 'A'	
30-40% cover	10-20%	70-80%	0-10%
Abies balsamea *Betula papyrifera* *Picea glauca (20%)*	*Betula papyrifera* *Populus tremuloides* *Rosa acicularis* *Sheperdia canadensis* *Viburnum trilobium*	*Anenome canadense* *Arctostaphylos rubra* *Cornus canadensis* *Cassiope tetregona* *Epilobium latifolium* *Equisetum sp.* *Iliamna rivularis* *Ledum groenlandicum* *Stipa sp.* *Vaccinium vitis-idaea*	*Hylocomium splendens* *Pleurozium schreberi* *Ptilium crista-castrensis*
		Site 'B'	
30-40% cover	20-30%	60-70%	10-20%
Abies balsamea *Betula papyrifera* *Picea glauca (20%)*	*Abies balsamea* *Betula papyrifera* *Rosa acicularis* *Viburnum trilobium*	*Arctostaphylos rubra* *Cornus canadensis* *Epilobium latifolium* *Equisetum sp.* *Iliamna rivularis* *Ledum groenlandicum* *Stipa sp.* *Vaccinium vitis-idaea*	*Hylocomium splendens* *Pleurozium schreberi* *Ptilium crista-castrensis*

Table B3. Plant Community Descriptions; Keg River Region (cont'd).

Site 'C'

30-40 cover	30-40%	70-80%	0-10%
Abies balsamea	*Betula papyrifera*	*Actaea rubra*	*Hylocomium splendens*
Betula papyrifera	*Populus tremuloides*	*Arctostaphylos rubra*	*Pleurozium schreberi*
Picea glauca (5%)	*Prunus virginiana*	*Clematis verticellaris*	*Ptilium*
Populus tremuloides	*Rosa acicularis*	*Cornus canadensis*	*crista-castrensis*
	Rubus strigosus	*Epilobium latifolium*	
	Viburnum trilobium	*Equisetum sp.*	
		Iliamna rivularis	
		Ledum groenlandicum	
		Ribes oxyacanthoides	

APPENDIX C

Soil Chemical Analyses

Table C1. Soil Chemical Analysis: pH and cation concentrations in soil samples from the Hinton region.
[1] mmol/g dry soil, [2]umol/g dry soil.

Site and (Pit No.)	Sample Depth (cm)	pH	NH_4-OAc extractable					KCl extractable
			Ca^1	Mg^1	Na^2	K^2	Fe^2	Al^2
HA(1)	15-25	8.04	0.2694	0.0420	1.17	2.56	0.29	0.13
	30-40	7.92	0.0671	0.0082	0.56	4.32	0.03	0.13
	50-60	7.99	0.0039	0.0053	0.47	8.62	0.01	0.13
	90-100	8.14	0.0946	0.0066	0.04	0.79	0.07	0.13
	110-120	8.21	0.0861	0.0049	0.04	0.54	0.02	0.06
HA(2)	10-20	8.10	0.3106	0.0461	0.56	2.25	0.48	0.13
	30-40	8.52	0.0738	0.0144	0.47	1.17	0.29	0.13
	50-60	8.14	0.0242	0.0074	0.04	0.66	0.04	0.06
	95-105	8.03	0.1846	0.0309	0.34	2.17	0.02	0.06
	120-130	8.10	0.2070	0.0325	0.26	1.92	0.02	0.06
HB(2)	0-10	8.14	0.1053	0.0053	1.28	0.74	0.17	0.13
	10-20	8.15	0.1198	0.0066	0.26	0.59	0.45	0.13
	20-30	8.33	0.1427	0.0066	0.34	0.43	0.32	0.13
	40-50	8.04	0.1290	0.0070	0.34	0.72	0.30	0.13
	80-90	8.17	0.1055	0.0053	0.34	0.56	0.02	0.06
	130-140	8.18	0.0155	0.0053	0.34	0.56	0.05	0.13
HC(1)	0-10	8.02	0.2495	0.0292	0.26	0.87	0.19	0.13
	20-30	8.38	0.1659	0.0119	0.26	0.54	0.15	0.13
	30-50	8.49	0.1176	0.0123	0.34	0.48	0.51	0.13
HC(2)	0-12	8.31	0.1866	0.0226	1.65	1.33	0.26	0.13
	12-27	8.06	0.1734	0.0210	0.04	0.74	0.12	0.06
	27-44	8.14	0.0271	0.0259	0.04	0.66	0.07	0.06
	44-51	8.14	0.1290	0.0107	0.04	1.99	0.05	0.06
	70-80	8.22	0.1509	0.0156	0.04	0.77	0.04	0.06
	90-110	8.16	0.1509	0.0078	0.21	0.87	0.03	0.06
	110-120	8.27	0.1290	0.0045	0.08	0.48	0.07	0.1297

Table C2. Soil Chemical Analysis: pH and cation concentrations in soil samples from the Whitecourt Region.
[1] mmol/g dry soil, [2] umol/g dry soil.

Site and (Pit No.)	Sample Depth (cm)	pH	NH_4-OAc extractable					KCl extractable
			Ca[1]	Mg[1]	Na[2]	K[2]	Fe[2]	Al[2]
WA(2)	0- 7	4.91	0.0197	0.0033	1.91	2.68	0.16	1.81
	7-21	5.88	0.0317	0.0049	0.65	2.35	0.16	2.47
	21-31	5.94	0.0609	0.0156	0.56	2.35	1.16	4.28
	31-54	5.59	0.0669	0.0189	0.82	2.60	0.02	4.13
	54-73	5.15	0.0626	0.0185	0.65	2.56	0.02	0.78
	73-90	5.10	0.0696	0.0210	0.82	2.61	0.02	0.25
	90-97	5.33	0.0674	0.0193	0.78	2.45	0.02	2.59
WB(1)	13-16	5.22	0.0234	.0.0066	0.82	1.58	0.10	2.11
	16-21	5.18	0.0644	0.0218	1.08	3.50	0.10	3.78
WB(2)	0-29	5.16	0.0472	0.0095	0.52	4.04	0.12	3.10
	29-33	5.51	0.0838	0.0185	1.30	3.50	0.28	2.43
	33-45	5.37	0.0878	0.0197	1.30	3.17	0.60	4.48
	45-61	5.37	0.0888	0.0185	1.65	2.94	0.26	5.49
	61-84	4.99	0.0873	0.0202	1.91	3.27	0.04	0.06
	84-112	7.68	0.1734	0.0222	1.39	2.53	0.02	0.25
WC(1)	0-12	4.81	0.0210	0.0082	1.91	3.09	0.48	2.11
	12-20	5.19	0.0656	0.0280	0.65	5.11	0.29	2.76
	20-40	5.08	0.0713	0.0329	0.91	4.09	0.17	6.70
	40-68	5.30	0.0644	0.0317	1.31	2.56	0.07	4.13
	68-90	5.30	0.0741	0.0350	1.52	2.58	0.03	0.06
	90-100	7.07	0.0753	0.0346	1.56	2.63	0.05	0.06
	100-110	7.80	0.0985	0.0353	1.52	2.56	0.03	0.06

Table C3. Soil Chemical Analysis: pH and cation concentrations in soil samples from the Keg River region.
[1] mmol/g dry soil, [2]umol/g dry soil.

Site and (Pit No.)	Sample Depth (cm)	pH	NH_4-OAc extractable					KCl extractable
			Ca[1]	Mg[1]	Na[2]	K[1]	Fe[2]	Al[2]
KA(1)	0-13	4.68	0.0092	0.0029	0.70	197	3.81	7.32
	13-21	4.89	0.0022	0.0074	0.52	2.61	0.52	23.37
	21-35	4.99	0.0347	0.0103	0.56	3.20	0.22	23.76
	35-53	4.86	0.0397	0.0119	0.74	3.20	0.22	19.33
	60-70	4.59	0.0427	0.0312	0.74	4.91	0.07	14.12
	70-80	5.03	0.0404	0.0111	0.61	2.22	0.03	8.52
	80-90	5.26	0.0451	0.0107	0.65	2.12	0.03	5.81
	100-110	5.69	0.0322	0.0053	0.35	1.35	0.04	0.31
KB(1)	0-15	5.26	0.0826	0.0197	0.52	5.37	0.26	0.13
	15-34	5.42	0.0202	0.0070	0.35	1.28	0.13	0.13
KB(2)	0-12	4.63	0.0142	0.0045	0.26	1.76	0.46	7.41
	12-30	5.10	0.0164	0.0062	0.39	1.51	0.74	6.43
	30-50	5.28	0.0334	0.0148	0.65	2.30	0.22	5.50
	50-70	5.34	0.0439	0.0189	0.43	2.45	0.02	3.11
	70-80	5.56	0.0556	0.0189	0.43	2.45	0.02	3.11
	80-90	5.73	0.0544	0.0222	0.56	2.58	0.02	0.99
	100-110	5.74	0.0639	0.0239	0.61	2.48	0.03	0.60
KC(1)	0-15	5.37	0.0581	0.0193	0.56	6.37	0.29	0.77
	15-34	5.04	0.0471	0.0325	5.65	5.93	0.54	7.20
	34-52	4.68	0.0447	0.0325	8.22	5.47	0.76	8.09
KC(2)	0-7	5.49	0.0619	0.0309	3.26	6.57	0.39	1.00
	7-38	5.05	0.0249	0.0185	1.17	5.65	0.25	7.91
	38-50	4.77	0.0369	0.0284	2.30	4.53	0.07	14.86
	50-60	4.80	0.0369	0.0288	2.70	4.40	0.09	14.86
	70-80	4.77	0.0427	0.0342	3.52	5.27	0.08	14.86
	100-110	4.67	0.0439	0.0334	4.69	5.63	0.05	12.71

Table C4. Soil chemical analysis: nitrogen and carbon concentrations in soil samples from the Hinton region.

Site and (Pit No.)	Sample depth(cm)	Nitrogen mg/g dry soil NH_4-N	NO_3-N	Carbon % by weight total C	org. C	inorg. C
HA(2)	10-20	1.44	0.11	11.700	10.844	0.816
	30-40	0.33	0.0	0.556	-	
	50-60	0.27	0.0	0.223	-	
	95-105	0.27	0.0	0.731	0.199	0.532
	120-130	0.23	0.0	1.142	0.376	0.766
HB(2)	0-10	0.64	0.0	7.676	5.898	0.178
	10-20	0.54	0.11	7.669	5.876	1.793
	20-30	0.51	0.22	7.387	5.600	1.787
	40-50	0.36	0.09	6.385	4.600	1.785
	80-90	0.40	0.08	5.787	4.002	1.785
	130-140	0.33	0.0	5.329	3.544	1.785
HC(2)	0-12	0.70	0.75	7.694	5.927	1.767
	12-27	0.70	0.36	6.608	4.844	1.764
	27-44	0.52	0.24	6.934	5.174	1.787
	44-51	0.46	0.10	6.158	4.370	1.788
	70-80	0.54	0.10	6.541	4.761	1.780
	90-110	0.29	0.0	0.603	0.552	0.053

Table C5. Soil chemical analysis: nitrogen and carbon concentrations of soil samples from the Whitecourt region.

Site and (Pit No.)	Sample depth(cm)	Nitrogen mg/g dry soil NH_4-N	NO_3-N	Carbon % by weight total C	org. C	inorg. C
WA(2)	0-7	0.60	0.0	1.101	1.015	0.086
	7-21	0.42	0.0	0.464	0.377	0.087
	21-31	0.49	0.0	0.354	0.217	0.137
	31-54	0.59	0.0	0.378	0.228	0.153
	54-73	0.70	0.0	0.300	0.166	0.159
	73-90	0.57	0.0	0.334	0.166	0.168
	90-97	0.53	0.0	0.300	0.134	0.166
WB(2)	0-29	0.54	0.0	0.697	0.597	0.100
	29-33	0.98	0.0	0.642	0.493	0.148
	33-45	0.76	0.0	0.564	0.396	0.168
	45-61	0.70	0.0	0.468	0.293	0.175
	61-84	0.62	0.0	0.431	0.244	0.186
	84-112	0.43	0.0	0.749	0.248	0.501
WC(1)	0-12	0.59	0.0	0.582	0.504	0.078
	12-20	0.54	0.0	0.688	0.533	0.155
	20-40	0.60	0.0	0.605	0.443	0.162
	40-68	0.73	0.0	0.552	0.393	0.159
	68-90	0.61	0.0	0.550	0.365	0.185
	90-100	0.30	0.0	0.481	0.268	0.213

Table C6. Soil chemical analysis: nitrogen and carbon concentration of soil samples from the Keg River region.

Site and (Pit no.)	Sample depth(cm)	Nitrogen mg/g dry soil NH_4-N	NO_3-N	Carbon % by weight total C	org. C	inorg. C
KA(1)	0-13	0.53	0.0	0.706	0.656	0.050
	13-21	0.65	0.0	0.686	0.607	0.079
	21-35	0.88	0.0	0.721	0.629	0.092
	35-53	0.95	0.0	0.550	0.454	0.096
	69-70	1.95	0.0	1.323	1.206	0.117
	80-90	0.54	0.0	0.402	0.280	0.122
KB(2)	0-12	0.48	0.0	1.399	0.040	
	12-30	0.32	0.0	0.462	0.366	0.060
	30-50	0.53	0.0	0.450	0.348	0.102
	50-70	0.61	0.0	0.583	0.448	0.145
	70-80	0.51	0.0	0.593	0.437	0.156
	80-90	0.46	0.0	0.534	0.367	0.167
KC(2)	0-7	1.28	0.0	3.732	3.610	
	7-38	0.53	0.0	0.831	0.763	0.068
	38-50	0.53	0.0	0.734	0.652	0.081
	50-60	0.80	0.0	0.686	0.595	0.091
	70-80	1.13	0.0	0.666	0.568	0.098
	100-110	1.27	0.0	0.696	0.592	0.099

APPENDIX D

Mother Tree Properties: Stem and Cone Characters.

Table D1. Mother tree stem dimensions and ages; Hinton sites.

Site	Tree Number	Number of Rings*	Height (m)	D.B.H. (cm)
HA	2	209(1.4 m)	20.7	31.3
	3	170	21.3	27.8
	5	257	17.5	24.1
	8	133	19.4	27.2
	14	143	17.4	26.7
	15	42	10.8	11.5
Average		159	17.8	24.8
HB	2	164	16.4	21.1
	4	174	15.4	17.0
	8	259	15.9	17.7
	12	256	18.8	22.8
	14	252(1.0 m)	19.9	31.9
	16	185	20.0	27.1
Average		215	17.7	22.9
HC	3	106	16.2	30.2
	5	214	17.4	21.5
	6	197	18.1	21.6
	7	191	15.0	20.3
	8	149	18.6	24.2
	10	213	12.6	17.4
	12	197	14.3	19.1
	13	192	16.8	17.6
	15	188	15.2	17.2
	18	176	17.1	21.7
Average		182	16.1	19.2

* Unless otherwise indicated, rings were counted on stumps 1.2 to 1.3 m. above ground. Numbers in brackets are stump heights beyond this range.

Table D2. Mother tree stem dimensions and ages; Whitecourt sites.

Site	Tree Number	Number of Rings*	Height (m)	D.B.H. (cm)
WA	4	83	24.2	32.8
	8	85(1.4 m)	24.4	26.7
	9	83	22.8	29.7
	14	87	22.8	26.4
	15	89	21.4	29.5
	17	88	22.5	25.1
Average		85.8	23.1	28.4
WB	2	99	23.8	27.4
	5	121	26.8	32.3
	6	107	26.5	34.3
	7	132	27.4	38.1
	8	134	32.6	58.2
	10	123	28.6	41.9
Average		119.3	27.6	38.7
WC	2	112	29.5	47.5
	3	106	27.1	37.6
	4	117	27.2	30.0
	8	111(1.4 m)	27.4	31.0
	10	109(0.8 m)	27.1	41.9
	15	97	22.2	25.2
Average		108.6	26.7	35.5

* Unless otherwise indicated, rings were counted on stumps 1.2 to 1.3 m. above ground. Numbers in brackets are stump heights beyond this range.

Table D3. Mother tree stem dimensions and ages; Keg River sites.

Site	Tree Number	Number of Rings*	Height (m)	D.B.H. (cm)
KA	1	83	20.9	30.5
	2	76	18.4	34.0
	3	74	21.0	27.9
	8	74	23.1	27.3
	9	79	24.7	30.6
	10	75	23.1	27.6
Average		76.8	21.9	29.6
KB	1	66	23.2	19.4
	6	73	24.1	23.1
	7	75	26.6	36.5
	8	77	24.2	27.1
	9	82	26.9	23.7
	10	79	23.9	32.7
Average		75.3	24.8	27.1
KC	4	56	19.5	18.6
	5	74	16.8	18.6
	6	78	21.6	34.8
	7	76	22.1	32.3
	8	66	14.4	23.0
	9	63	14.9	19.8
Average		68.8	18.2	24.5

* Unless otherwise indicated, rings were counted on stumps 1.2 to 1.3 m. above ground. Numbers in brackets are stump heights beyond this range.

Table D4. Seed weight index; all regions. Weight of 100 seeds in milligrams.

Site	HA	HB	HC	WA	WB	WC	KA	KB	KC
Tree no.									
1	265.6	233.0		185.6	166.8	94.6	159.2	165.6	144.0
2	233.2	248.4		232.4	181.2	150.0	128.8	168.8	248.8
3	269.6	228.8		227.6	160.0	220.0	198.8	246.8	139.6
4	212.8	231.5		168.7	106.0	168.0	208.3	195.2	292.0
5	235.2		343.6	214.0	131.6	112.4	184.4	176.0	222.8
6	210.8	276.8		188.9	170.4	160.4	157.6	172.0	276.0
7	234.2	244.0			185.6	200.0	253.6	184.3	195.2
8	304.8	253.2	301.3		179.2	146.4	185.6	154.8	240.3
9	255.2		292.8	253.2	181.2	119.2	181.7	184.8	143.5
10	275.6	199.4		262.8	184.8	158.4	187.2	210.4	161.6
11		314.8		223.6	219.6	163.2	195.6	247.2	150.7
12	232.8		302.0	281.2		166.4	152.0	213.2	250.3
13	276.4		248.8	222.8	215.2			195.6	121.6
14	264.0	241.6			120.8	168.4	162.8	225.2	252.0
15	379.2	327.6	303.2	205.4	140.4	160.1	250.2	188.4	
16	273.6	259.2	205.8	201.2	176.8	173.6			
17		233.2	282.4						
18			253.2	192.0					
19				160.4					
Max.	379.2	327.6	343.6	281.2	219.6	220.0	253.6	247.2	292.0
Min.	210.8	199.4	205.8	160.4	106.0	94.6	128.8	154.8	121.6
Range	168.4	128.2	137.8	120.8	113.6	125.4	124.8	92.4	170.4
Med.	264.8	244.0	292.8	214.0	173.5	160.4	185.0	188.4	205.3
Ave.	277.2	253.2	280.0	214.7	168.0	156.2	185.5	195.2	202.7

Table D5. Cone lengths; all regions.
Average of 15 cones in centimeters.

Site	HA	HB	HC	WA	WB	WC	KA	KB	KC
Tree No.									
1	3.7	3.6	4.3	3.9	3.4	2.4	3.4	4.3	3.3
2	3.5	4.3	3.8	4.7	4.3	2.9	3.8	4.8	4.4
3	3.5	4.1	4.2	3.7	3.2	3.8	3.9	4.6	3.5
4	3.6	4.2	4.3	4.5	3.3	3.3	4.5	5.2	4.3
5	3.7	3.6	3.5	4.4	2.6	2.7	3.8	6.5	4.5
6	3.4	4.1	4.3	3.3	4.4	3.6	3.9	3.4	4.4
7	3.3	3.9	3.8	4.0	3.2	3.5	4.3	5.1	4.0
8	4.4	4.0	4.5	4.7	4.4	3.0	3.5	5.3	4.8
9	4.3	4.1	3.5	3.5	3.8	3.1	4.1	4.2	3.6
10	4.1	3.3	4.3	3.9	3.9	3.6	3.5	4.3	3.5
11	4.0	4.9		3.9	4.3	2.8	5.0	5.6	4.4
12	4.2	3.6		4.3	3.2	4.2	3.8	4.9	4.3
13	3.3	3.6		3.8	3.4	4.0	3.5	5.2	3.5
14	4.6			3.8	4.0	3.5	4.3	4.7	4.5
15	3.6			3.4	3.2		4.4		
16	3.6			3.8					
Max.	4.6	4.3	4.5	4.7	4.4	4.2	5.0	6.5	4.8
Min.	3.3	3.3	3.5	3.3	2.6	2.4	3.4	3.4	3.3
Range	1.3	1.0	1.0	1.4	1.8	1.8	1.6	3.1	1.5
Med.	3.65	4.00	4.25	3.90	3.40	3.40	3.90	4.85	4.30
Ave.	3.81	3.95	4.06	3.98	3.65	3.49	3.98	4.87	4.08

APPENDIX E

Site Locations Within Regions and Mother Tree Locations Within Sites.

Figure E1. Site locations in the Hinton region.

Hinton site 'A' Township 50 Range 26
Lat. 53° 20"N Long. 117° 44"W
Elevation 990m (±10m)

Hinton site 'B' Township 51 Range 27
Lat. 53° 18"N Long. 117° 49"W
Elevation 1050m (±10m)

Hinton site 'C' Township 49 Range 27
Lat. 53° 14"N Long. 117° 49"W
Elevation 1070m (±10m)

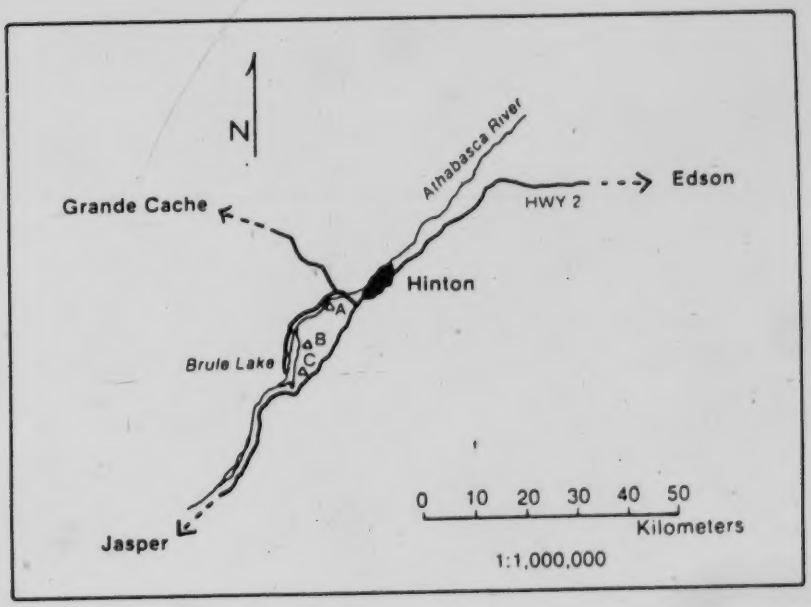

Figure E2. Site locations in the Whitecourt region.

Whitecourt site 'A' Township 62 Range 11
Lat. 54° 21"N Long. 115° 34"W
Elevation 930m (±10m)

Whitecourt site 'B' Township 63 Range 12
Lat. 54° 25"N Long. 115° 43"W
Elevation 990m (±10m)

Whitecourt site 'C' Township 61 Range 12
Lat. 54° 11"N Long. 115° 50"W
Elevation 920m (±10m)

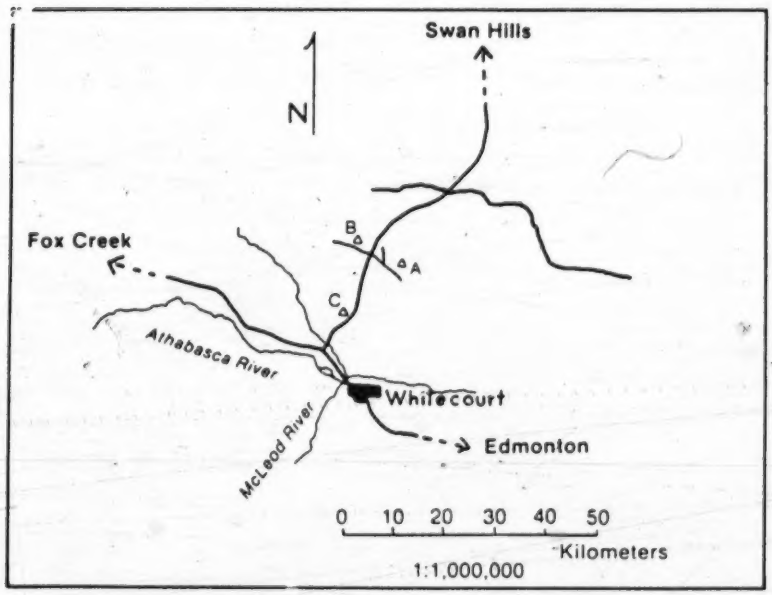

Figure E3. Site locations in the Keg River Region.

Keg River site 'A' Township 100 Range 21
Lat. 57° 39'N Long. 117° 25'W
Elevation 710m (±10m)

Keg River site 'B' Township 99 Range 21
Lat. 57° 37'N Long. 117° 26'W
Elevation 690m (±10m)

Keg River site 'C' Township 100 Range 23
Lat. 57° 41'N Long. 117° 43'W
Elevation 680m (±10m)

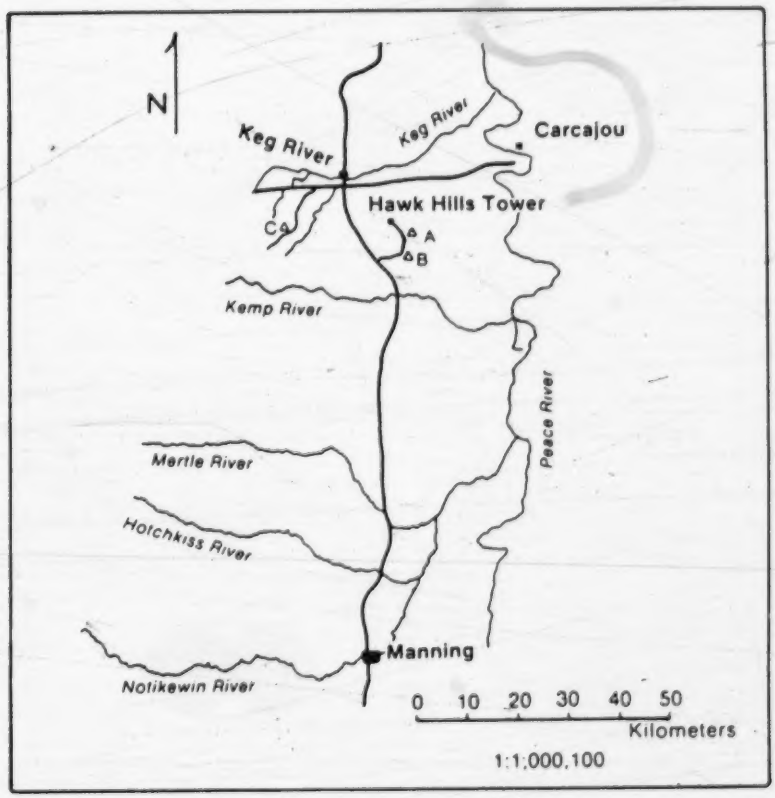

Figure E4. Mother tree locations; Hinton site 'A'.

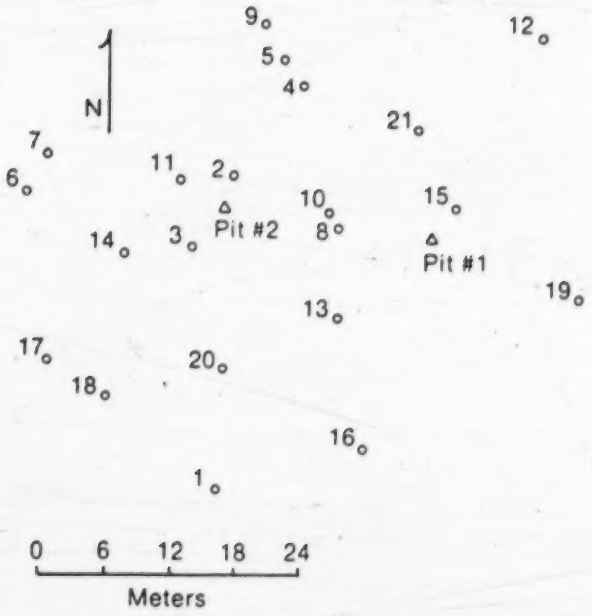

Figure E5. Mother tree locations; Hinton site 'B'.

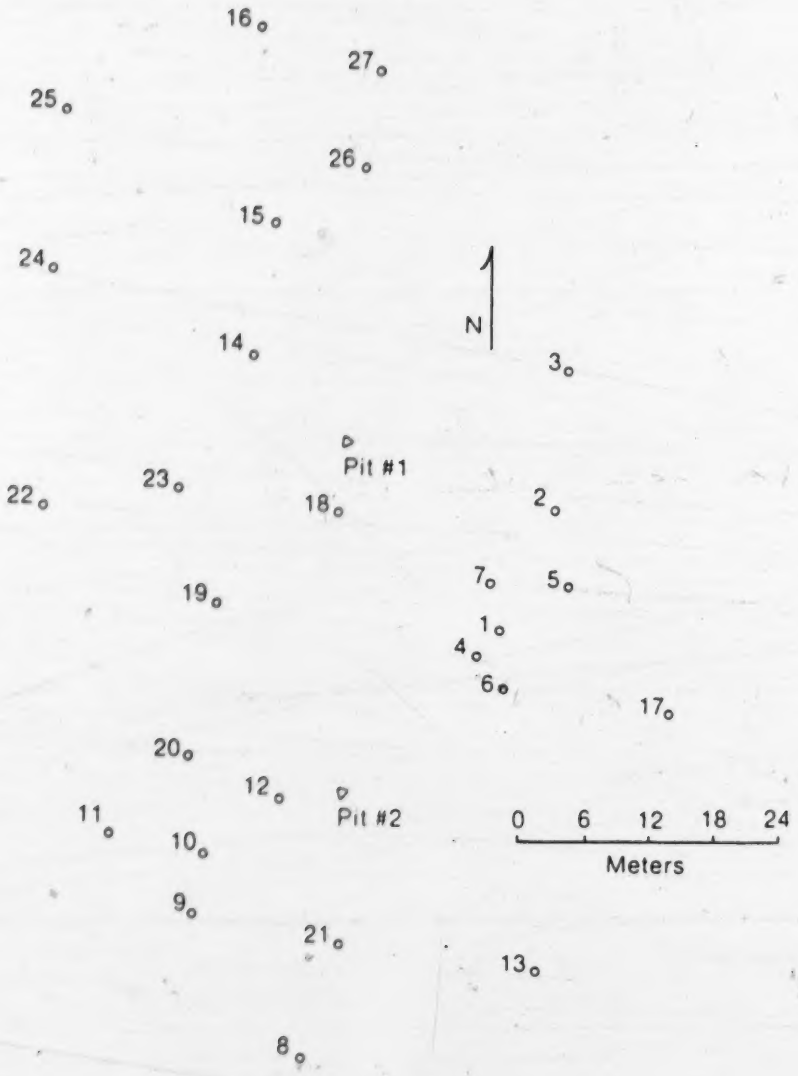

Figure E6. Mother tree locations; Hinton site 'C'.

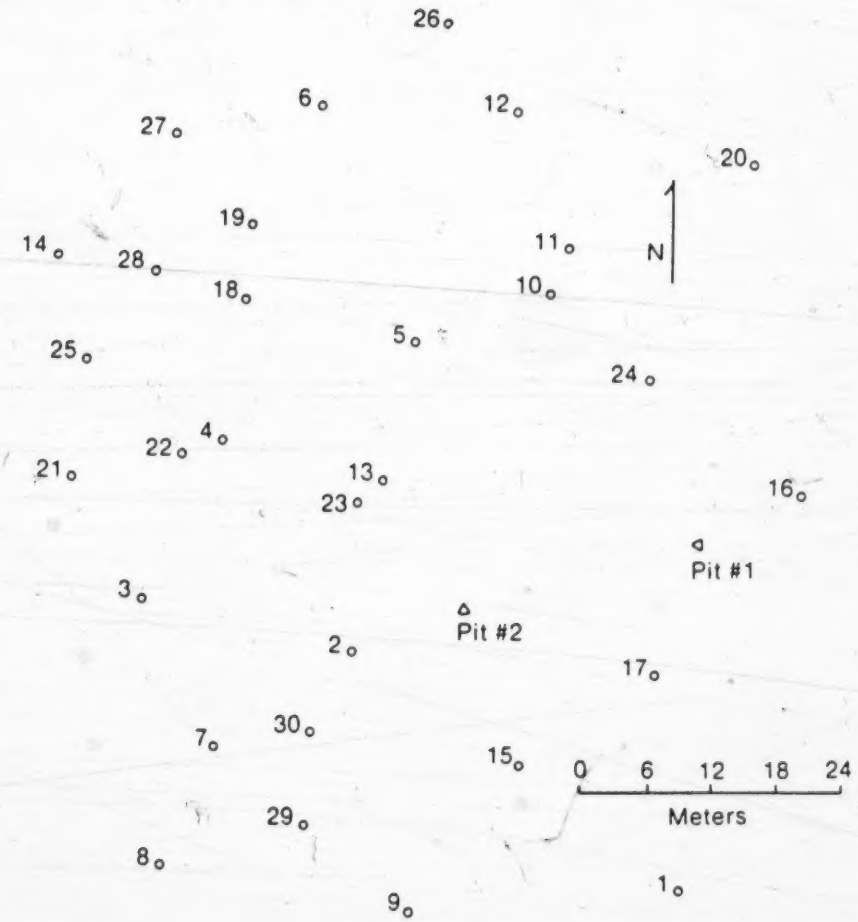

Figure E7. Mother tree locations; Whitecourt site 'A'.

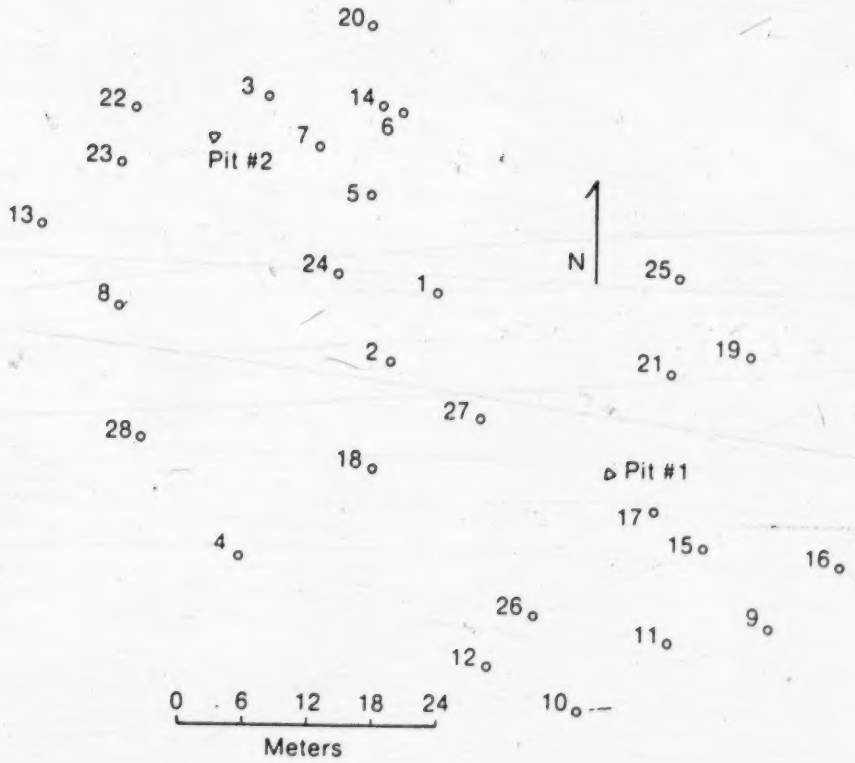

Figure E8. Mother tree locations; Whitecourt site 'B'.

Figure E9. Mother tree locations; Whitecourt site 'C'.

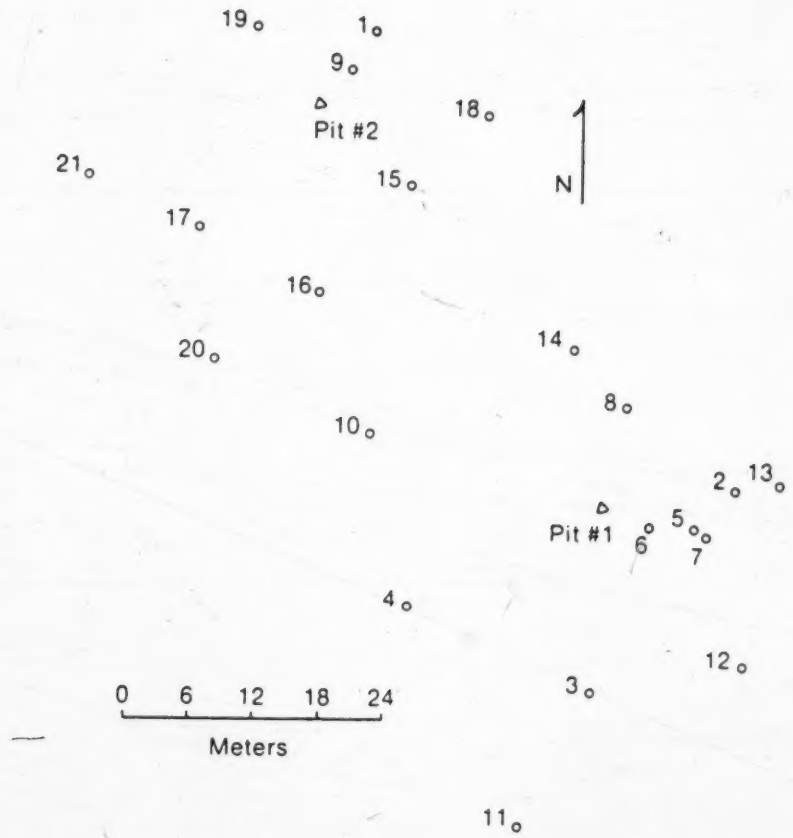

Figure E10. Mother tree locations; Keg River site 'A'.

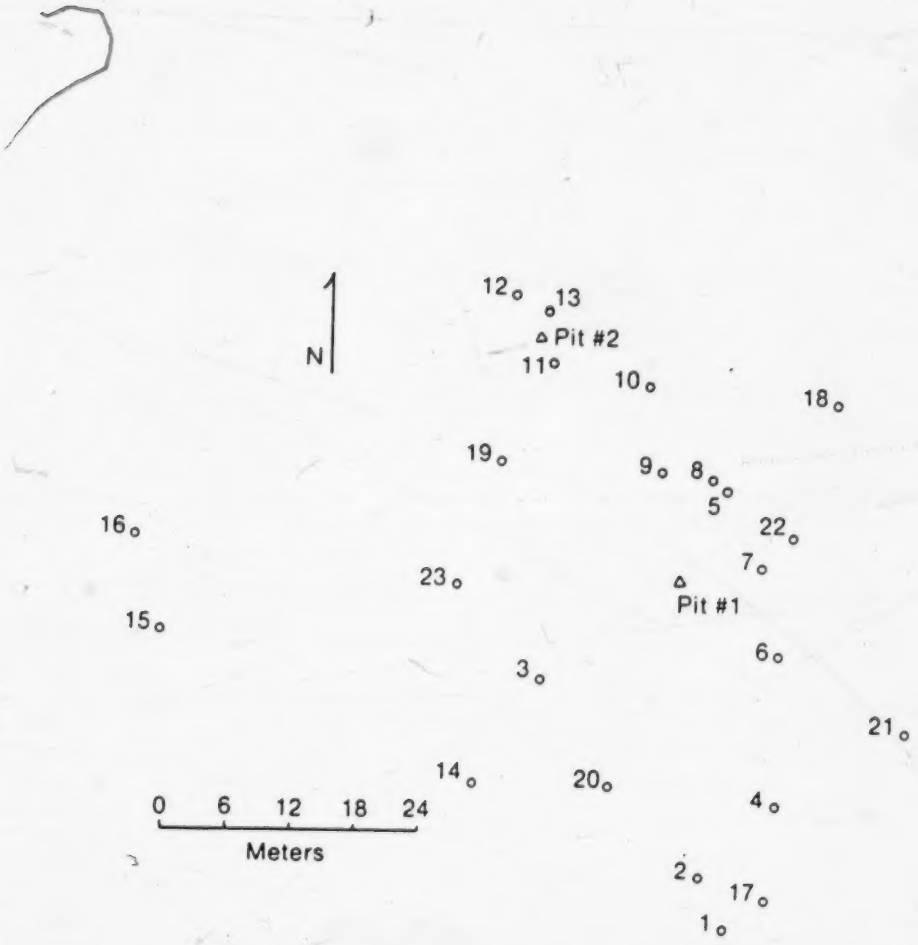

Figure E11. Mother tree locations; Keg River site 'B'.

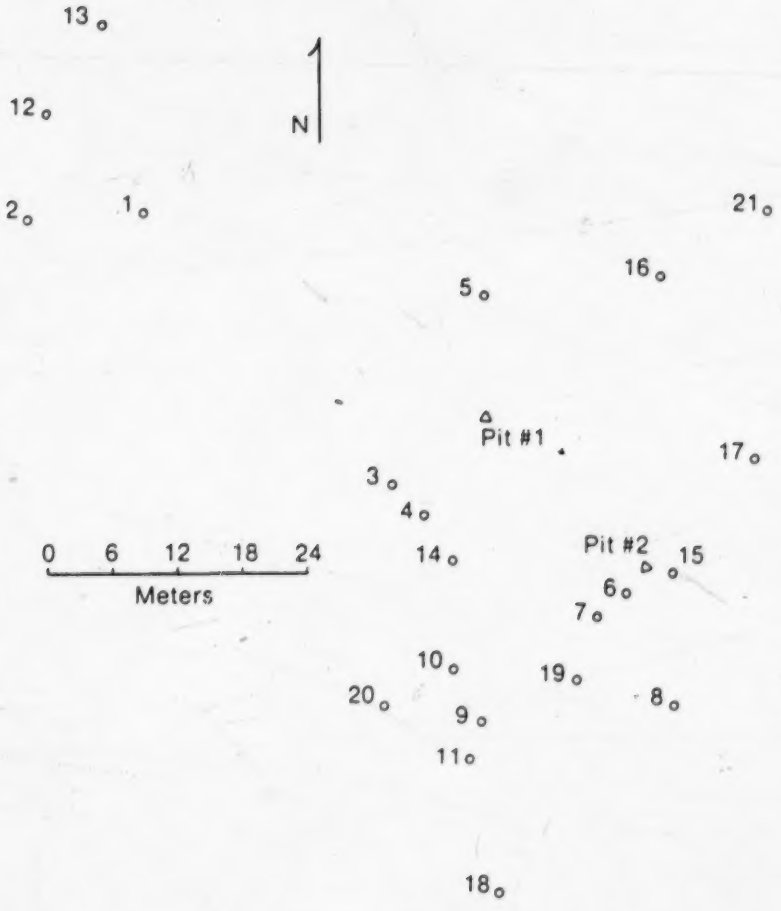

Figure E12. Mother tree locations; Keg River site 'C'.

APPENDIX F

Procedures for preparation of nutrient solutions

Procedure for composing nutrient solutions in the gravel culture progeny test.

Total volumes for each of the three treatments was 135 L.

Step 1

With 135 L distilled water in each drum, one drum per treatment, add the following:

35.710 g NH_4NO_3

5.568 g K_2HPO_4

0.477 g NaCl

0.143 g H_3BO_3

20.8 mg Mn-EDTA[1]

17.2 mg Cu-EDTA[1]

17.8 mg Zn-EDTA[1]

0.1 mg Mo-EDTA[1]

Step 2

The following amounts of compounds, in grams, were also added to the respective treatments ('Hinton', 'Whitecourt' and 'Keg River' treatments are designated as 'H', 'W' and 'K'):

CHEMICAL	SOLUTION H	W	K
$CaSO_4$	63.69	31.84	15.71
Mg-HEEDA[1]	33.33	30.30	27.27
Fe-HEEDA[1]	7.32	14.63	29.95
$Al_2(SO_4)_3$	0.16	4.79	13.16
pH	7.7	6.2	4.7

PH was adjusted to proper values with HCl or KOH.

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[1]Chelates supplied by Golden-West Seed Co., Calgary, Alberta. Atomic absorption analysis indicated metal concentrations (% by weight) of 12.0, 14.5, 14.0, 39.0, and 10.25 % in Mn, Cu, Zn, Mo, and Fe chelates, respectively.

Procedure for composing nutrient solutions for the hydroponics progeny tests.

Step 1

Prepare the following stock solutions in 1 l glass or plastic containers:

Solution A. 1.0 M $Ca(NO_3)_2$ —	236.00 g/liter distilled water
Solution B. 1.0 M NH_4NO_3 —	80.04 g/l distilled water
Solution C. 1.0 M $MgSO_4$ —	120.40 g/l distilled water
Solution D. 1.0 M K_2HPO_4 —	174.20 g/l distilled water
Solution E. Fe-HEEDA —	220.45 g/l distilled water
Solution G. Micronutrients	0.725 g Cu-EDTA/l 22.250 g Mn-EDTA/l 2.018 g Zn-EDTA/l 0.066 g Mo-EDTA/l
Solution H. Aluminum	175.075 g $Al_2(SO_4)_3$/500 ml

Step 2

Add stock solutions to 108 liters of feed solution as follows:

add 54 ml each of solutions A, B and C

add 27 ml of solution D

add 20 ml each of solutions E, F and G

add 20 ml of solution H to aluminum treatments only

APPENDIX G

Analysis of Variance Tables For Progeny Tests.

Soil composite progeny test

* * * ANALYSIS OF VARIANCE * * *

TOTAL DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	9989784.333	4	2497441.083	57.047	0.000
REGION	208620.312	2	104310.156	2.383	0.093
TREATMENT	9939991.630	2	4969980.815	113.528	0.000
2-WAY INTERACTIONS	23353.205	4	5838.301	0.133	0.970
REGION TREATMENT	23353.205	4	5838.301	0.133	0.970
EXPLAINED	10013117.539	8	1251639.692	28.590	0.000
RESIDUAL	35768830.205	817	43778.372		
TOTAL	45780047.743	825	55490.967		

ABOVE GROUND DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	2799516.053	4	699879.517	51.586	0.000
REGION	97376.769	2	48688.384	3.589	0.028
TREATMENT	2748377.814	2	1374188.957	101.282	0.000
2-WAY INTERACTIONS	17452.507	4	4363.127	0.322	0.864
REGION TREATMENT	17452.507	4	4363.127	0.322	0.864
EXPLAINED	2816970.575	8	352121.322	25.956	0.000
RESIDUAL	11083932.471	817	13568.625		
TOTAL	13900903.046	825	16849.579		

RATIO OF ABOVE TO BELOW GROUND DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	2.848	4	0.662	1.706	0.146
REGION	2.103	2	1.051	2.713	0.067
TREATMENT	0.599	2	0.300	0.773	0.462
2-WAY INTERACTIONS	1.032	4	0.258	0.666	0.618
REGION TREATMENT	1.032	4	0.258	0.666	0.618
EXPLAINED	3.880	8	0.460	1.187	0.304
RESIDUAL	316.357	817	0.387		
TOTAL	320.237	825	0.388		

LEAF WEIGHT INDEX
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	38997.351	4	9749.338	21.572	0.000
REGION	17376.456	2	8688.234	19.586	0.000
TREATMENT	24016.848	2	12008.326	26.571	0.000
2-WAY INTERACTIONS	637.586	4	159.398	0.353	0.842
REGION TREATMENT	637.586	4	159.398	0.353	0.842
EXPLAINED	39634.987	8	4954.373	10.963	0.000
RESIDUAL	369230.572	817	451.935		
TOTAL	408865.559	825	495.595		

836 CASES WERE PROCESSED.

BY ROOT DRY WEIGHT
REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	2342686.195	4	585671.549	49.594	0.000
REGION	40502.452	2	20251.226	1.715	0.167
TREATMENT	2235648.847	2	1117824.424	99.065	0.000
2-WAY INTERACTIONS	13319.296	4	3329.824	0.295	0.881
REGION TREATMENT	13319.296	4	3329.824	0.295	0.881
EXPLAINED	2356005.493	8	282000.687	24.994	0.000
RESIDUAL	9217812.503	817	11282.512		
TOTAL	11473817.995	825	13907.658		

BY LEAF DRY WEIGHT
REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	1085226.897	4	271306.724	48.493	0.000
REGION	85443.661	2	42721.831	7.636	0.001
TREATMENT	1037180.512	2	518590.256	92.692	0.000
2-WAY INTERACTIONS	3166.712	4	791.678	0.142	0.967
REGION TREATMENT	3166.712	4	791.678	0.142	0.967
EXPLAINED	1088393.610	8	136049.201	24.317	0.000
RESIDUAL	4570936.855	817	5594.782		
TOTAL	5659330.465	825	6859.795		

BY ROOT COLLAR DIAMETER
REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	181824.071	4	45456.018	40.772	0.000
REGION	8193.264	2	4096.142	3.674	0.026
TREATMENT	177673.061	2	88836.530	79.670	0.000
2-WAY INTERACTIONS	7873.087	4	1968.272	1.765	0.133
REGION TREATMENT	7873.087	4	1968.272	1.765	0.133
EXPLAINED	189697.158	8	23587.145	21.270	0.000
RESIDUAL	909659.119	817	1113.659		
TOTAL	1099356.277	825	1332.553		

BY STEM HEIGHT
REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	130431.677	4	32607.885	33.680	0.000
REGION	1554.948	2	777.474	0.803	0.448
TREATMENT	126827.461	2	63913.731	66.030	0.000
2-WAY INTERACTIONS	1339.831	4	334.958	0.346	0.848
REGION TREATMENT	1339.831	4	334.958	0.346	0.848
EXPLAINED	131771.509	8	16471.439	17.104	0.000
RESIDUAL	786778.888	817	963.010		
TOTAL	918550.397	825	1113.394		

825 CASES WERE PROCESSED

gravel culture progeny test

* * * A N A L Y S I S O F V A R I A N C E * * *

TOTAL DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	98019.295	4	24004.824	2.728	0.026
REGION	33600.024	2	16800.012	1.906	0.149
TREATMENT	61492.801	2	30746.401	3.493	0.031
2-WAY INTERACTIONS	18237.583	4	4559.396	0.518	0.723
REGION TREATMENT	18237.583	4	4559.396	0.518	0.723
EXPLAINED	114256.878	8	14282.110	1.622	0.118
RESIDUAL	6902682.940	784	8804.443		
TOTAL	7016939.818	792	8859.772		

ABOVE GROUND DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	77024.338	4	19256.084	3.298	0.011
REGION	25832.683	2	12786.341	2.188	0.113
TREATMENT	51988.731	2	25994.365	4.452	0.012
2-WAY INTERACTIONS	8804.108	4	1851.027	0.283	0.889
REGION TREATMENT	8804.108	4	1851.027	0.283	0.889
EXPLAINED	83828.442	8	10482.555	1.780	0.078
RESIDUAL	4577793.081	784	5839.022		
TOTAL	4661621.523	792	5885.633		

ROOT DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	3591.455	4	897.887	1.478	0.207
REGION	2888.867	2	1444.434	2.377	0.094
TREATMENT	490.305	2	245.103	0.403	0.668
2-WAY INTERACTIONS	2944.046	4	736.011	1.211	0.305
REGION TREATMENT	2944.046	4	736.011	1.211	0.305
EXPLAINED	6535.515	8	816.939	1.344	0.218
RESIDUAL	476424.419	784	607.684		
TOTAL	482959.934	792	609.798		

RATIO of ABOVE TO BELOW GROUND DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	131.159	4	32.790	10.970	0.000
REGION	48.438	2	24.219	8.102	0.000
TREATMENT	78.549	2	39.275	13.705	0.000
2-WAY INTERACTIONS	9.248	4	2.311	0.807	0.521
REGION TREATMENT	9.248	4	2.311	0.807	0.521
EXPLAINED	130.405	8	16.301	5.688	0.000
RESIDUAL	2246.645	784	2.865		
TOTAL	2377.050	792	3.001		

793 CASES WERE PROCESSED

gravel culture progeny test

* * * A N A L Y S I S O F V A R I A N C E * * *

LEAF DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	75391.148	4	18847.787	4.026	0.003
REGION	19825.124	2	9912.562	2.096	0.124
TREATMENT	56224.602	2	28112.401	6.005	0.003
2-WAY INTERACTIONS	5046.733	4	1261.683	0.270	0.898
REGION TREATMENT	5046.733	4	1261.683	0.270	0.898
EXPLAINED	80437.881	8	10054.735	2.148	0.029
RESIDUAL	3670085.970	784	4681.232		
TOTAL	3750523.851	792	4735.510		

AVERAGE VIGOR
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	15.399	4	3.850	5.772	0.000
REGION	2.348	2	1.173	1.759	0.173
TREATMENT	13.089	2	6.545	9.813	0.000
2-WAY INTERACTIONS	6.612	4	1.653	2.478	0.043
REGION TREATMENT	6.612	4	1.653	2.478	0.043
EXPLAINED	22.011	8	2.751	4.126	0.000
RESIDUAL	522.669	784	0.667		
TOTAL	544.680	792	0.688		

ROOT COLLAR DIAMETER
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	13412.801	4	3353.200	5.891	0.000
REGION	3123.954	2	1561.982	2.744	0.065
TREATMENT	10576.941	2	5288.471	9.292	0.000
2-WAY INTERACTIONS	670.747	4	167.687	0.295	0.882
REGION TREATMENT	670.747	4	167.687	0.295	0.882
EXPLAINED	14083.548	8	1760.443	3.093	0.002
RESIDUAL	446295.582	784	569.255		
TOTAL	460379.130	792	581.287		

STEM HEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	966.495	4	241.624	3.797	0.005
REGION	477.056	2	238.528	3.748	0.024
TREATMENT	495.015	2	247.507	3.889	0.021
2-WAY INTERACTIONS	142.950	4	35.738	0.562	0.691
REGION TREATMENT	142.950	4	35.738	0.562	0.691
EXPLAINED	1109.445	8	138.681	2.179	0.027
RESIDUAL	49892.340	784	63.636		
TOTAL	51001.788	792	64.396		

793 CASES WERE PROCESSED.

Hydroponics progeny test

* * * ANALYSIS OF VARIANCE * * *

LEAF DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	1526218.483	3	508406.184	3.988	0.008
REGION	321429.644	2	160714.772	1.284	0.286
TREATMENT	1203788.819	1	1203788.819	9.398	0.002
2-WAY INTERACTIONS	187932.448	2	93966.224	0.733	0.481
REGION TREATMENT	187932.448	2	93966.224	0.733	0.481
EXPLAINED	1713150.811	5	342630.162	2.674	0.021
RESIDUAL	68415630.022	534	128118.157		
TOTAL	70128780.833	539	130109.058		

BRANCH NUMBER INCREMENTS
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	34.472	3	11.491	3.521	0.015
REGION	12.470	2	6.235	1.910	0.149
TREATMENT	22.002	1	22.002	6.741	0.010
2-WAY INTERACTIONS	15.004	2	7.502	2.299	0.101
REGION TREATMENT	15.004	2	7.502	2.299	0.101
EXPLAINED	49.476	5	9.895	3.032	0.010
RESIDUAL	1742.855	534	3.264		
TOTAL	1792.331	539	3.325		

STEM HEIGHT INCREMENTS
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	4337.839	3	1445.946	2.954	0.032
REGION	1424.459	2	712.230	1.454	0.156
TREATMENT	2913.380	1	2913.380	5.935	0.024
2-WAY INTERACTIONS	2440.904	2	1220.452	2.493	0.084
REGION TREATMENT	2440.904	2	1220.452	2.493	0.084
EXPLAINED	8778.743	5	1755.749	2.770	0.018
RESIDUAL	261398.033	534	489.506		
TOTAL	268176.776	539	497.541		

BRANCH LENGTH INCREMENTS
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	26417.117	3	8139.039	2.197	0.087
REGION	11946.700	2	5973.350	1.613	0.200
TREATMENT	12470.417	1	12470.417	3.367	0.067
2-WAY INTERACTIONS	8001.211	2	4000.605	1.080	0.340
REGION TREATMENT	8001.211	2	4000.605	1.080	0.340
EXPLAINED	32418.328	5	6483.666	1.751	0.121
RESIDUAL	1977870.256	534	3703.877		
TOTAL	2010288.583	539	3729.663		

540 CASES WERE PROCESSED.

hydroponics progeny test

* * * A N A L Y S I S O F V A R I A N C E * * *

TOTAL DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	2381303.700	3	793767.900	2.878	0.036
REGION	153563.226	2	76781.613	0.278	0.757
TREATMENT	2227740.474	1	2227740.474	8.076	0.005
2-WAY INTERACTIONS	613565.715	2	306782.857	1.112	0.330
REGION TREATMENT	613565.715	2	306782.857	1.112	0.330
EXPLAINED	2994869.415	5	598973.883	2.172	0.056
RESIDUAL	147293987.222	534	275831.437		
TOTAL	150288856.637	539	278828.048		

ABOVE GROUND DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	1905348.648	3	635116.216	3.131	0.025
REGION	246007.348	2	123003.824	0.606	0.546
TREATMENT	1659341.300	1	1659341.400	8.180	0.004
2-WAY INTERACTIONS	359983.544	2	179991.772	0.887	0.412
REGION TREATMENT	359983.544	2	179991.772	0.887	0.412
EXPLAINED	2265332.193	5	453066.439	2.233	0.050
RESIDUAL	108325171.356	534	202856.126		
TOTAL	110590503.548	539	205177.187		

ROOT DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	91237.344	3	30412.448	3.469	0.016
REGION	48454.937	2	24727.469	2.821	0.060
TREATMENT	41782.407	1	41782.407	4.766	0.029
2-WAY INTERACTIONS	40439.448	2	20219.724	2.307	0.101
REGION TREATMENT	40439.448	2	20219.724	2.307	0.101
EXPLAINED	131676.793	5	26335.359	3.004	0.011
RESIDUAL	4680994.844	534	8765.908		
TOTAL	4812671.637	539	8928.890		

RATIO of ABOVE TO BELOW GROUND DRY WEIGHT
BY REGION
TREATMENT

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
MAIN EFFECTS	855.821	3	285.274	4.885	0.002
REGION	813.714	2	406.857	6.939	0.001
TREATMENT	42.107	1	42.107	0.718	0.397
2-WAY INTERACTIONS	82.323	2	41.162	0.702	0.496
REGION TREATMENT	82.323	2	41.162	0.702	0.496
EXPLAINED	938.144	5	187.629	3.200	0.007
RESIDUAL	31309.927	534	58.633		
TOTAL	32248.071	539	59.829		

540 CASES WERE PROCESSED

APPENDIX H

Seed Source Site Means Versus Treatment Means

and

Stem Height Versus Root Collar Diameter

Figure H1. Seed source site means versus treatment means; total dry weight in the soil composite progeny test. Performance mean of each seed source are plotted against the treatment means for the experiment.

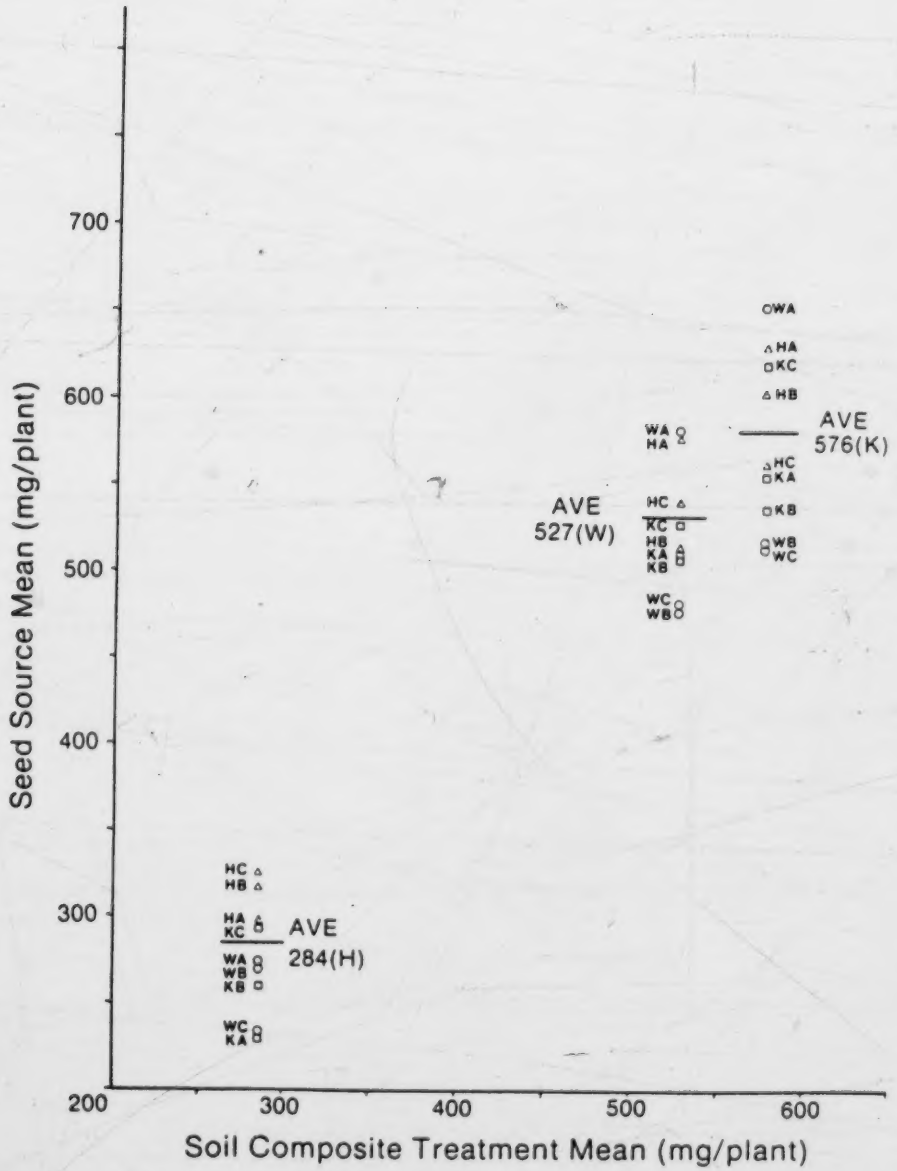


Figure H2. Seed source site means versus treatment means; root dry weight in the soil composite progeny test. Performance means of each seed source are plotted against the treatment means for the experiment.

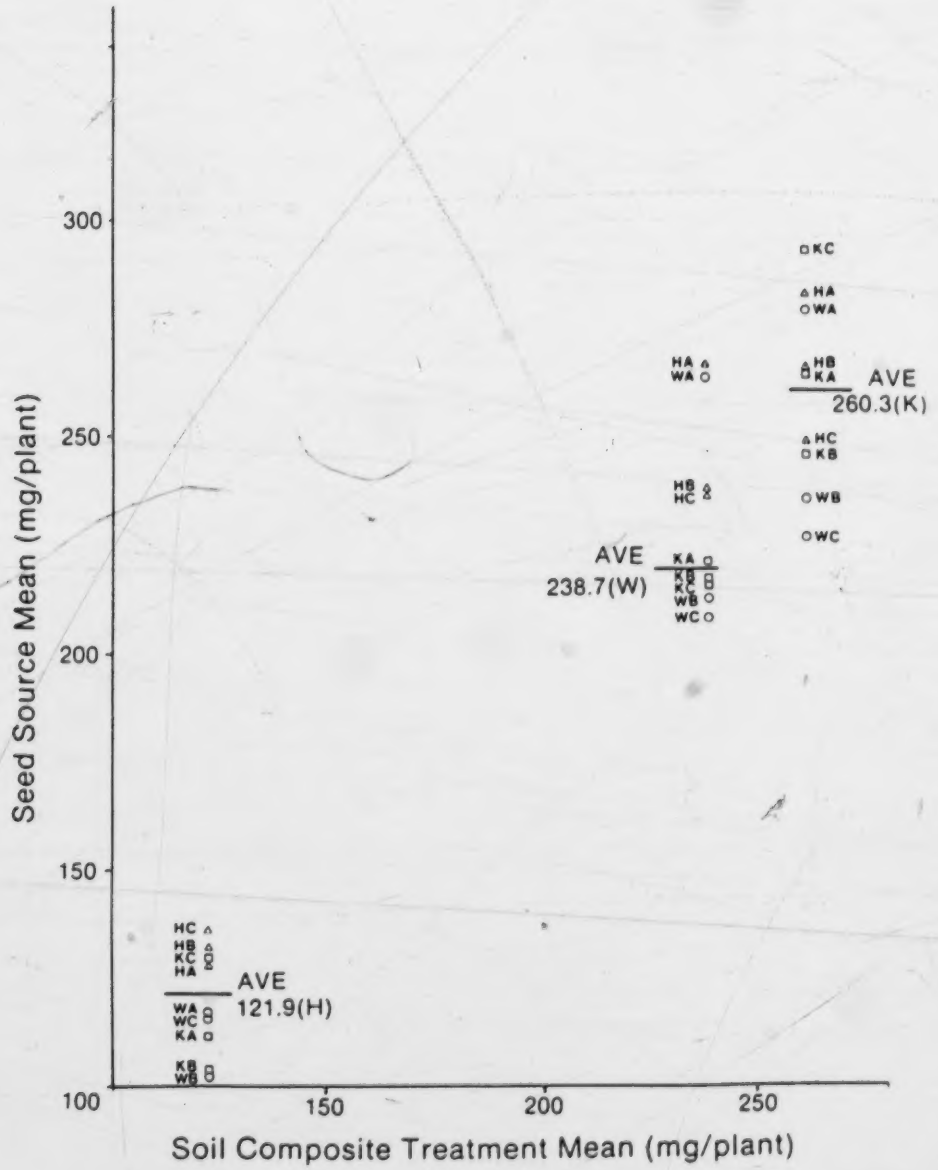


Figure H3. Seed source site means versus treatment means; above-ground dry weight in the soil composite progeny test. Performance means of each seed source are plotted against the treatment means for the experiment.

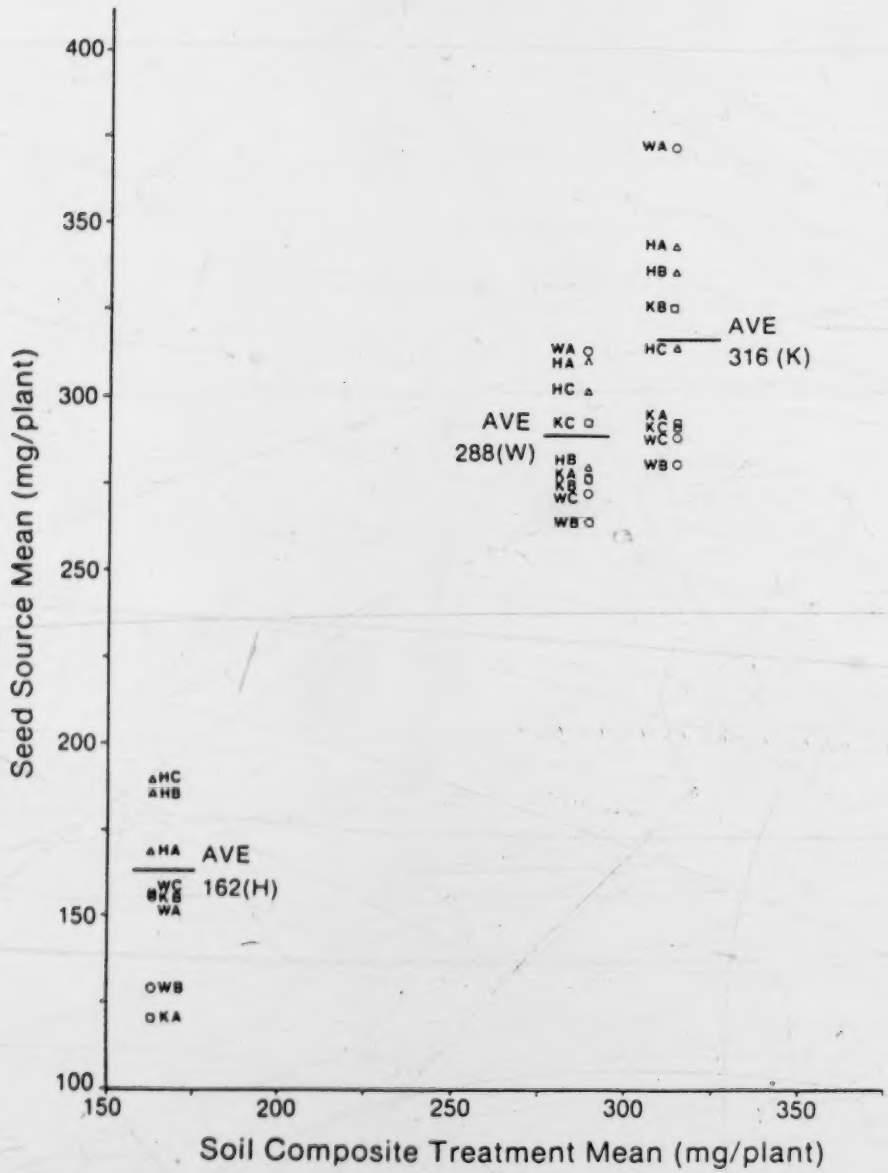


Figure H4. Seed source site means versus treatment means; leaf dry weight in the soil composite progeny test. Performance means of each seed source are plotted against the treatment means for the experiment.

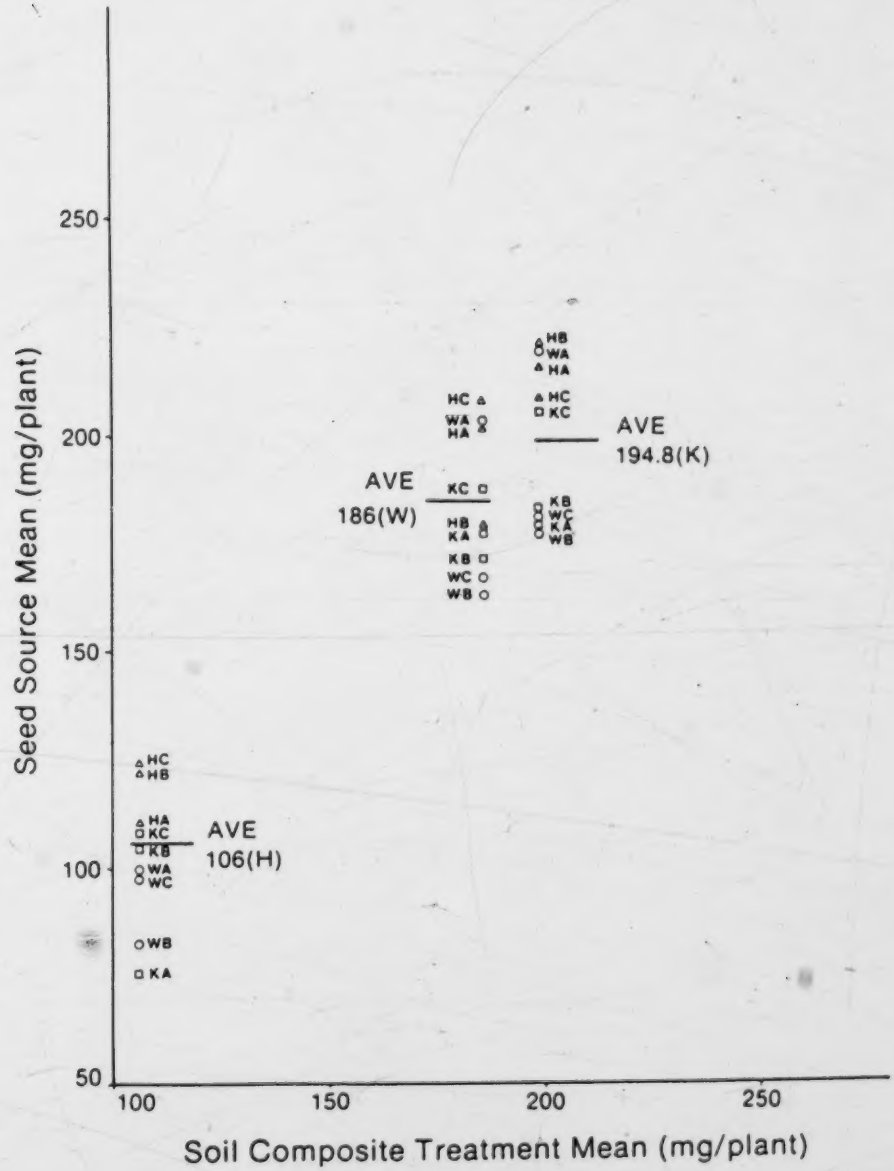


Figure H5. Seed source site means versus treatment means; leaf weight index in the soil composite progeny test. Performance means of each seed source are plotted against the treatment means for the experiment.

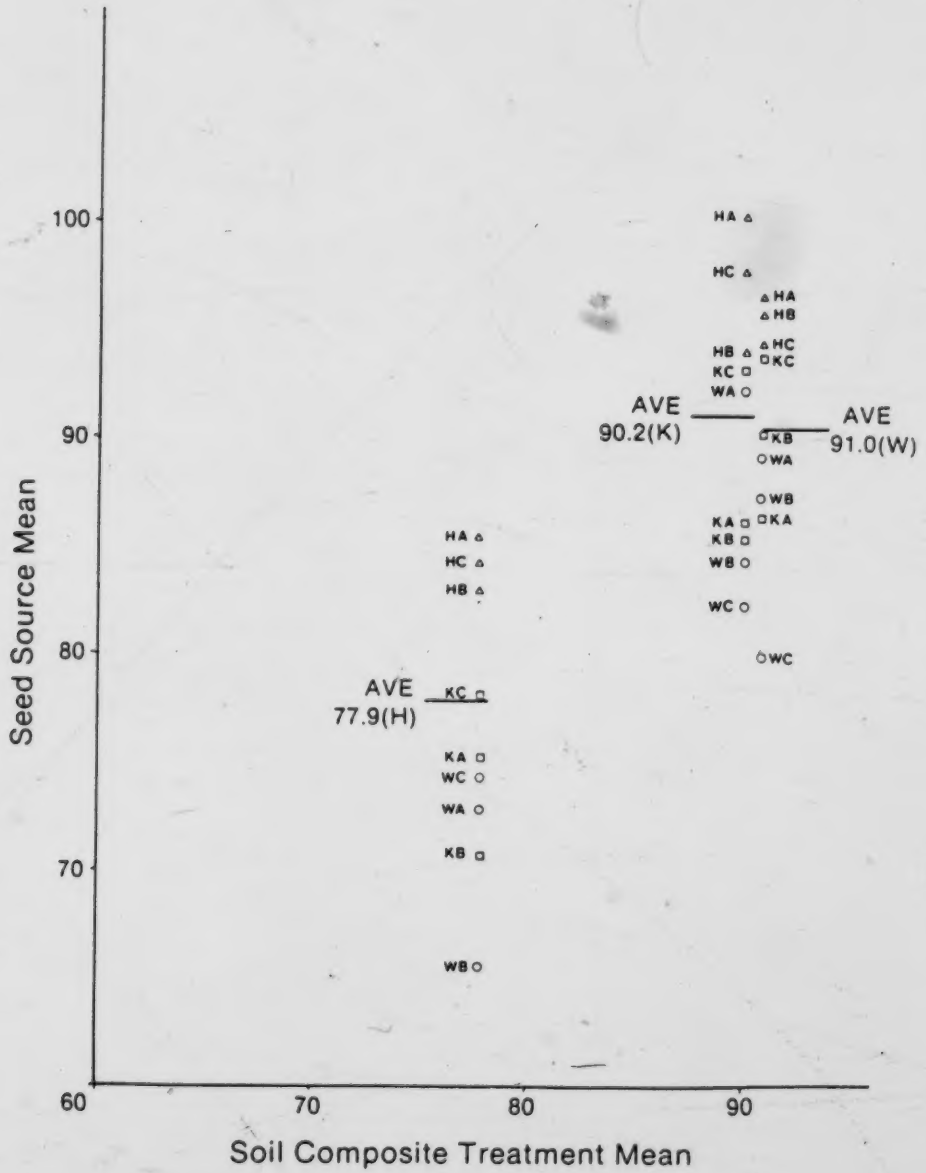


Figure H6. Seed source site means versus treatment means; total dry weight in the hydroponic progeny test. Performance means of each seed source are plotted against the treatment means for the experiment.

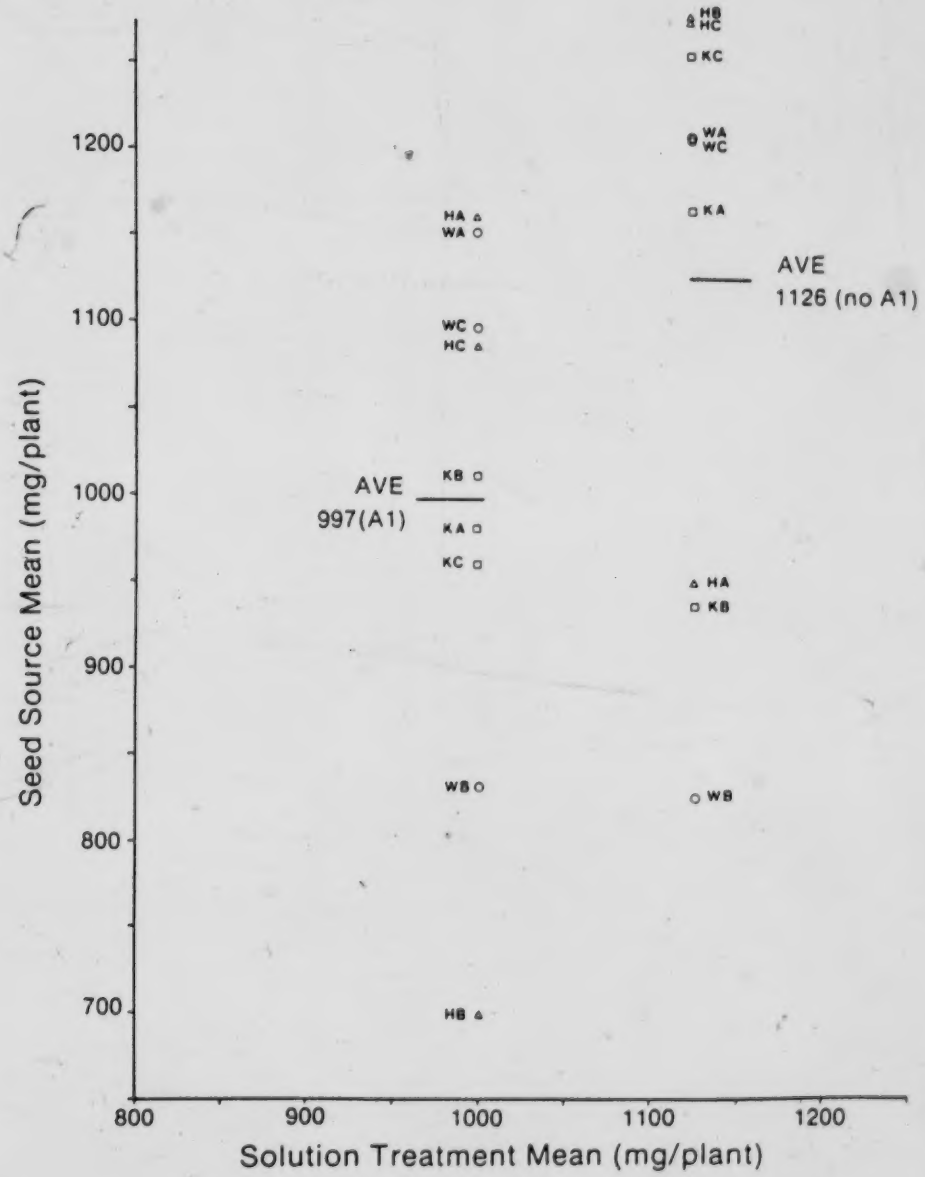


Figure H7. Seed source site means versus treatment means; root dry weight in the hydroponic progeny test. Performance means of each seed source are plotted against the treatment means for the experiment.

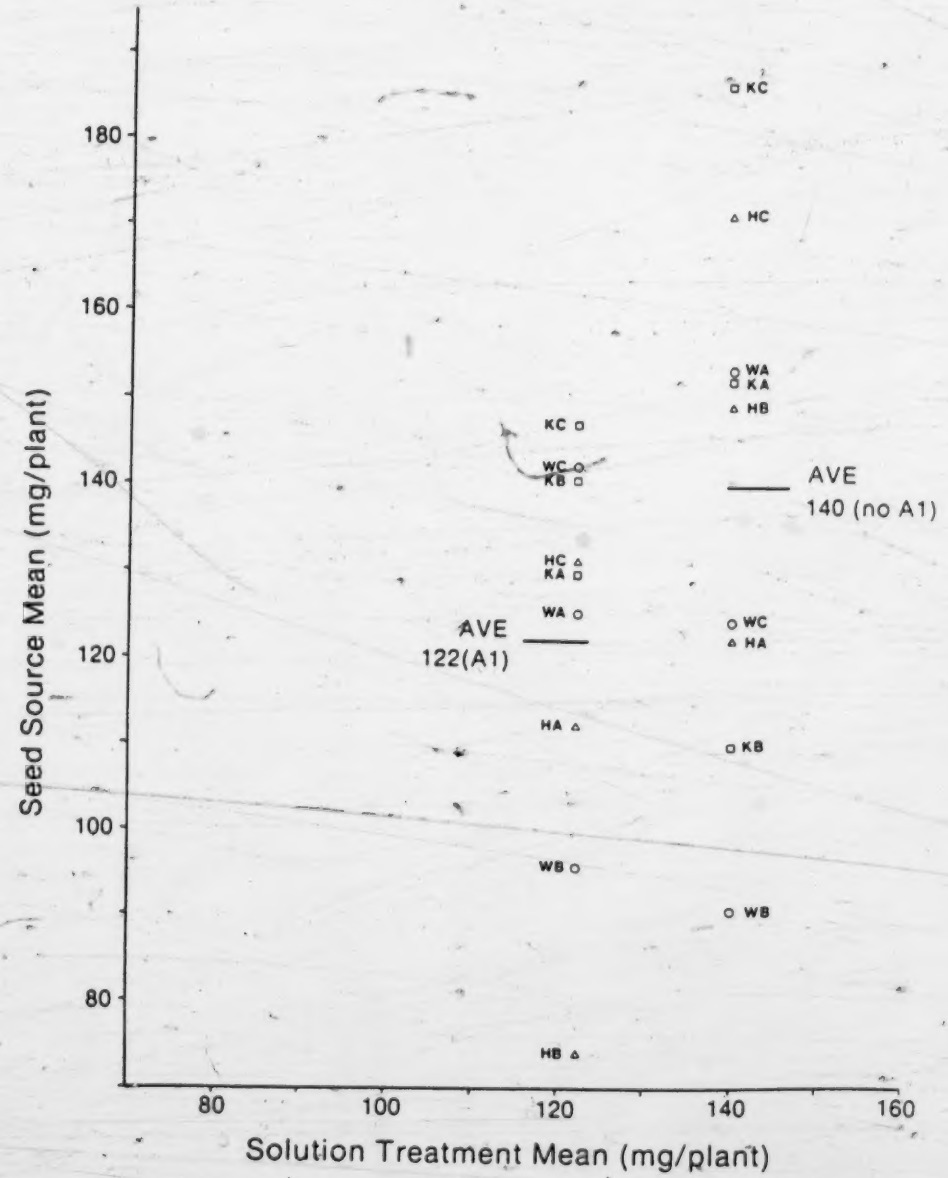


Figure H8. Seed source site means versus treatment means; above-ground dry weight in the hydroponic progeny test. Performance means of each seed source are plotted against the treatment means for the experiment.

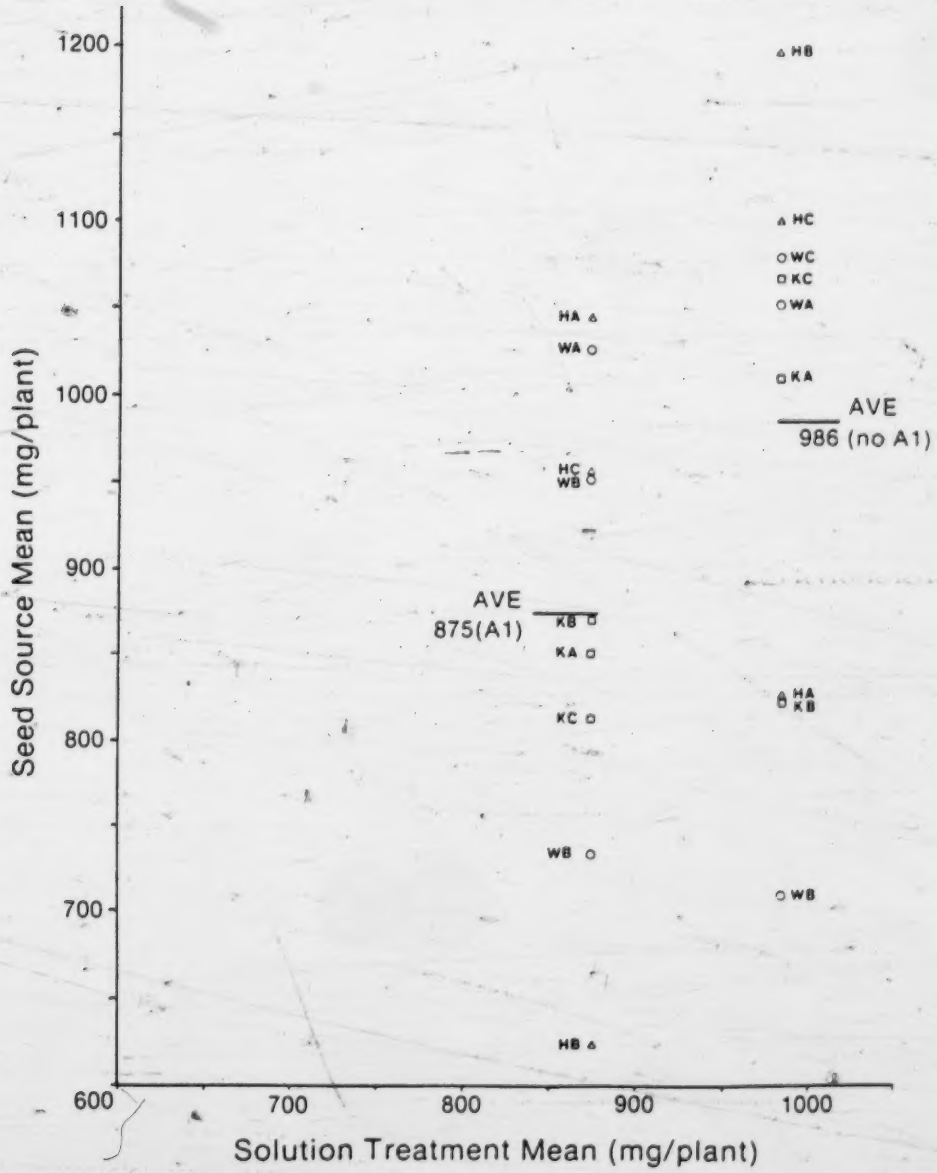


Figure H9. Seed source site means versus treatment means; leaf dry weight in the hydroponic progeny test. Performance means of each seed source are plotted against the treatment means for the experiment.

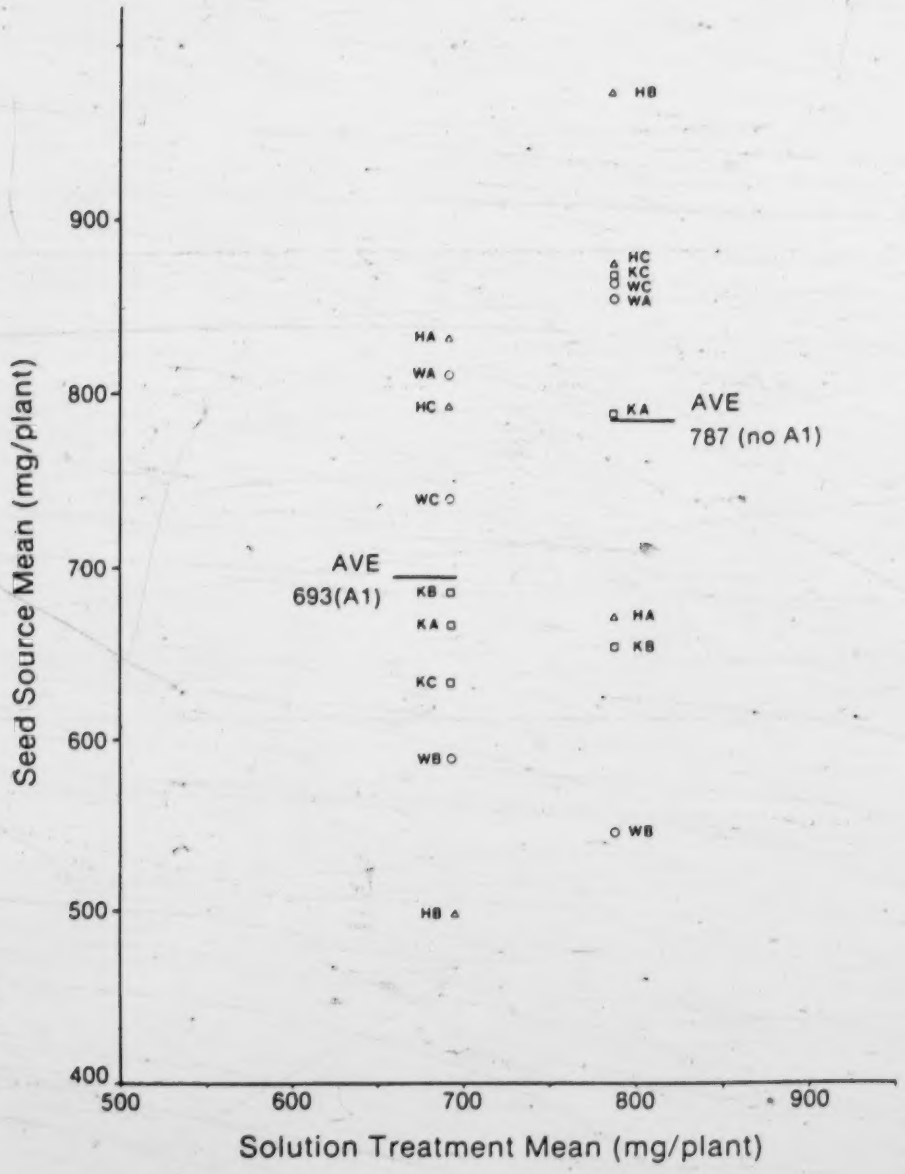


Figure H10. Stem height versus root collar diameter; Hinton treatment means in the soil composite progeny test.

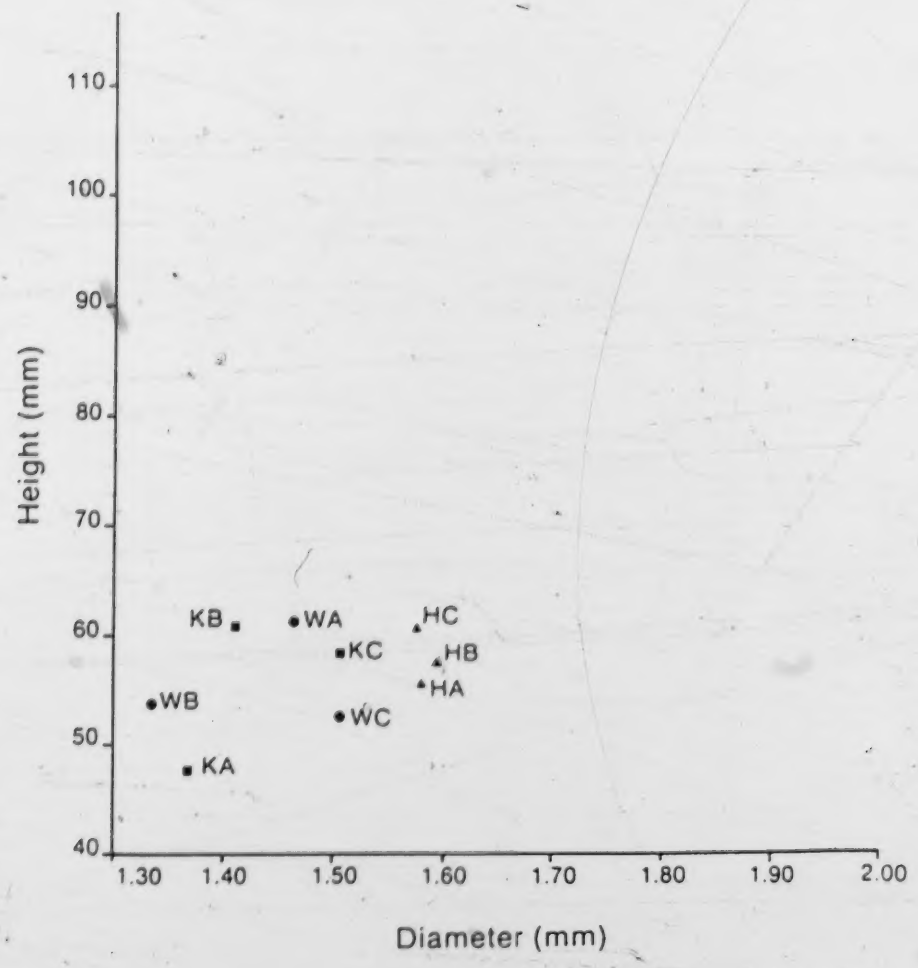


Figure H11. Stem height versus root collar diameter; Whitecourt treatment means in the soil composite progeny test.

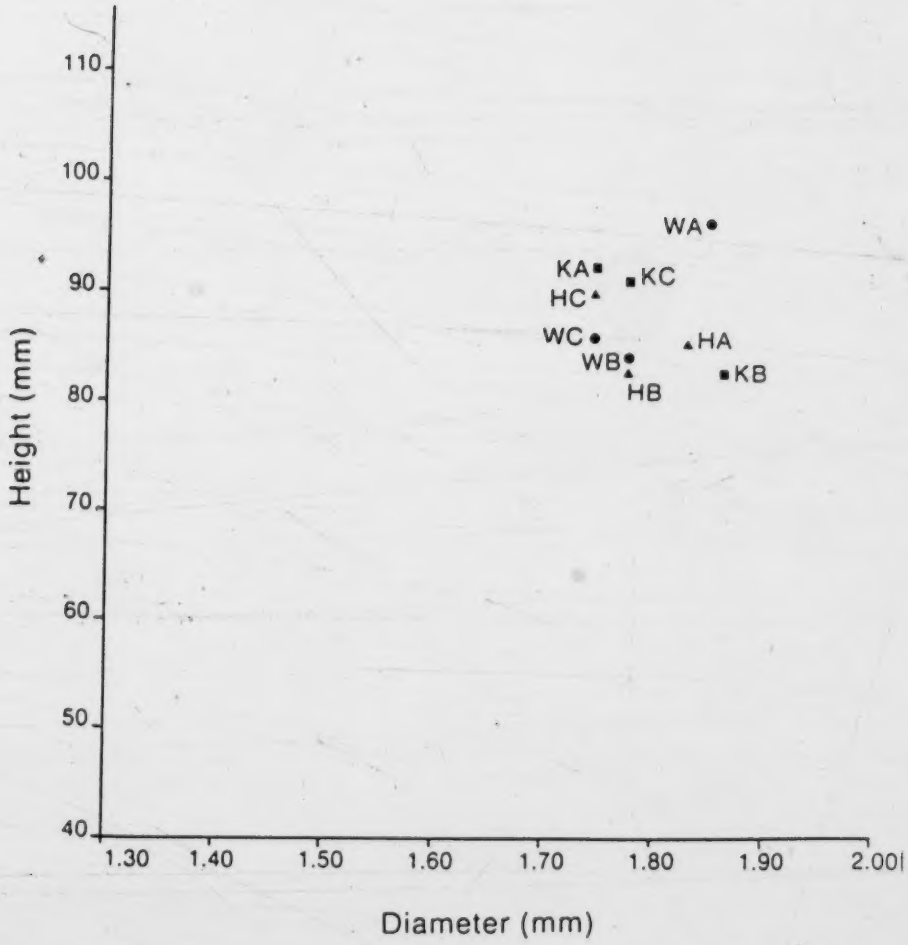
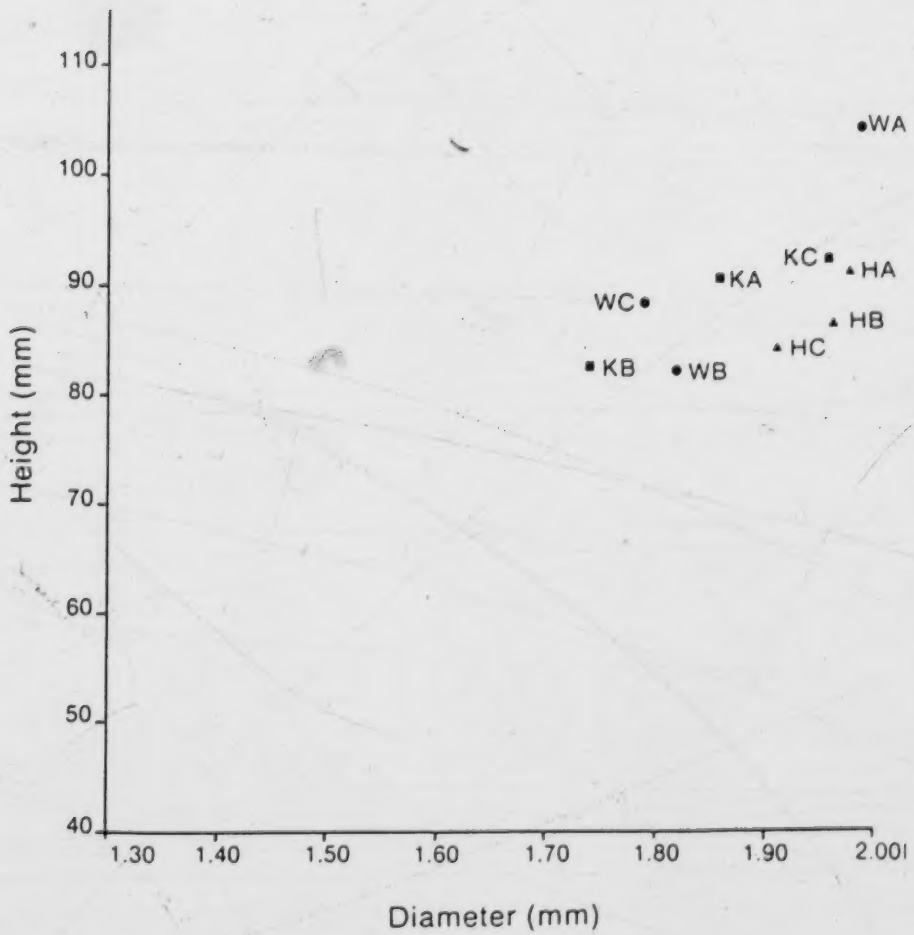


Figure H12. Stem height versus root collar diameter; Keg River treatment means in the soil composite progeny test.



APPENDIX I

Foliar analyses

Table I1. Foliar analyses; Hinton seedlings of the gravel culture progeny test. Seedling family and treatment are indicated. Text in parentheses refers to position of needle sample on stem and presence of chlorosis or necrosis. Records with no text are of green needle samples from the mid-stem position. 'T' indicates needle tip sample. 'U' indicates upper-stem needle sample. 'L' indicates-lower stem needle sample. 'C' indicates chlorotic needle sample. 'N' indicates necrotic needle sample.

Seedling Family and Treatment	% (dry weight basis)			ug/g dry weight			%
	Ca	Mg	K	Mn	Al	Fe	Ash
HA 21 on 'W'	1.27	0.16	0.34	189	93	118	5.08
HA 9 on 'K'	1.08	0.17	0.52	207	106	139	5.05
HA 21 on 'K'	0.73	0.09	0.23	156	156	128	3.29
HB 24 on 'H'	1.15	0.15	0.51	205	137	212	4.63
HB 24 on 'W'	1.21	0.13	0.54	120	146	184	5.31
HB 24 on 'W'	0.63	0.09	0.30	136	155	133	4.75
HB 24 on 'K'	1.13	0.18	0.59	246	103	167	5.34
HB 22 on 'H'	1.69	0.18	0.27	194	187	252	6.19
HB 22 on 'W'	1.13	0.15	0.38	203	170	210	5.20
HB 22 on 'K'	1.54	0.19	0.41	308	243	258	6.22
HB 24 on 'K' (T)	1.13	0.18	0.59	246	103	167	5.34
HB 24 on 'K' (T)	1.20	0.15	0.52	220	117	137	2.03
HB 21 on 'K' (U,C)	1.21	0.16	0.45	246	98	165	5.32
HB 21 on 'K' (L,C)	0.65	0.13	0.59	225	131	168	3.83
HC 15 on 'H' (N)	1.30	0.16	0.43	231	134	176	5.43
HC 15 on 'H'	1.31	0.17	0.66	111	223	291	5.62
HC 15 on 'W'	0.90	0.15	0.54	192	126	171	3.84
HC 15 on 'W'	1.13	0.14	0.44	156	623	898	6.75
HC 15 on 'K'	1.66	0.21	0.52	220	464	972	8.28
HC 15 on 'K'	1.51	0.21	0.32	242	428	775	8.47
HC 15 on 'K' (U,C)	1.49	0.20	0.54	230	204	311	4.42
HC 24 on 'H' (U,C)	0.60	0.06	0.32	62	59	70	3.48
HC 30 on 'W' (U,C)	0.40	0.07	0.46	97	162	185	2.64
HC 30 on 'W'	0.92	0.12	0.45	163	216	265	4.78

Table I2. Foliar analyses; Whitecourt seedlings of the gravel culture progeny test. Seedling family and treatment are indicated. Text in parenthese refers to position of needle sample on the stem and presence of chlorosis or necrosis. Records with no text are of green needles sampled from the midstem position. 'T' indicates needle tips sampled. 'U' indicates upper-stem needle sample. 'L' indicates lower-stem sample. 'C' indicates chlorotic needle sample. 'N' indicates necrotic needle sample.

Seedling family and treatment	% (dry weight basis) Ca	Mg	K	ug/g dry weight Mn	Al	Fe	% Ash
WA 22 on 'H' (C)	0.38	0.06	0.46	61	77	92	3.80
WA 22 on 'H'	0.88	0.11	0.32	124	69	72	3.42
WA 22 on 'W'	0.70	0.09	0.33	143	111	138	2.99
WA 22 on 'K'	0.77	0.12	0.37	248	264	127	3.38
WA 12 on 'H'	0.85	0.13	0.40	153	127	109	3.60
WA 12 on 'W'	1.16	0.16	0.40	255	147	153	3.08
WA 28 on 'W'	1.08	0.19	0.74	330	123	204	5.00
WA 28 on 'K'	0.95	0.14	0.52	233	388	726	5.85
Wa 28 on 'K' (C)	1.09	0.15	0.54	245	176	192	4.56
WA 6 on 'K'	1.07	0.16	0.60	229	93	168	4.48
WB 10 on 'H'	1.11	0.15	0.32	219	148	280	4.52
WB 10 on 'W' (C)	0.98	0.12	0.48	139	116	166	5.07
WB 10 on 'W'	1.70	0.25	0.50	245	196	237	7.17
WB 20 on 'K'	1.14	0.20	0.47	217	199	274	4.83
WB 20 on 'K'	1.05	0.15	0.46	317	124	170	
WC 10 on 'H'	1.35	0.20	0.51	411	200	259	5.88
WC 10 on 'W'	0.87	0.13	0.56	215	226	268	4.24
WC 10 on 'K'	0.93	0.15	0.43	161	495	332	6.02
WC 16 on 'H'	0.87	0.10	0.43	195	98	114	3.72
WC 16 on 'K'	0.96	0.16	0.32	264	129	187	3.95
WC 17 on 'W' (C)	0.80	0.12	0.41	90	119	153	3.50
WC 17 on 'W'	1.44	0.17	0.43	207	111	131	5.25

Table I3. Foliar analyses; Keg River seedlings of the gravel culture progeny test. Seedling family and treatment are indicated. Text in parentheses refers to position of needle sample on stem and presence of chlorosis or necrosis. Records with no text are of green needles sampled from the mid-stem position. 'T' indicates needle tip sample. 'U' indicates upper-stem needle sample. 'L' indicates lower-stem needle sample. 'C' indicates chlorotic needle sample. 'N' indicates necrotic needle sample.

Seedling family and treatment	% (dry weight basis) Ca	Mg	K	ug/g dry weight Mn	Al	Fe	% ash
KA 17 on 'H'	0.47	0.06	0.25	71	57	61	1.97
KA 15 on 'W'	0.96	0.13	0.40	204	130	118	3.66
KA 14 on 'W'	1.05	0.15	0.46	136	313	247	4.62
KA 12 on 'K'	1.55	0.21	0.48	389	211	295	5.54
KA 18 on 'H' (C)	0.66	0.08	0.34	118	64	120	2.95
KA 18 on 'H'	1.39	0.18	0.54	215	97	197	6.41
KA 18 on 'H'	1.25	0.17	0.50	276	265	432	4.39
KA 18 on 'W'	0.51	0.08	0.24	126	115	152	3.80
KA 18 on 'K' (C)	0.60	0.10	0.47	140	79	103	2.84
KA 18 on 'K'	1.27	0.20	0.51	236	183	210	5.10
KB 14 on 'H'	1.77	0.17	0.42	287	191	263	6.98
KB 14 on 'W' (N)	0.88	0.12	0.49	149	84	129	3.63
KB 14 on 'K'	1.11	0.15	0.33	272	141	208	3.52
KB 13 on 'H'	0.73	0.08	0.52	105	163	154	3.33
KB 21 on 'H'	0.97	0.16	0.39	197	164	222	4.18
KB 21 on 'W'	1.28	0.17	0.37	145	116	187	4.53
KB 21 on 'K'	1.74	0.28	0.51	339	232	334	5.18
KC 20 on 'H'	0.97	0.16	0.39	197	164	222	4.18
KC 20 on 'K'	1.74	0.29	0.61	563	160	292	7.55
KC 17 on 'W'	1.41	0.19	0.67	151	231	264	5.88
KC 5 on 'H'	0.75	0.10	0.39	144	135	195	3.71
KC 5 on 'K'	1.70	0.18	0.37	163	324	660	7.09
KC 5 on 'K'	1.06	0.16	0.48	225	137	272	4.66